

A review of the genera of the Hydroptilidae (Trichoptera)

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Synopsis

The Hydroptilidae, a world-wide group of small caddis flies, are reviewed down to the generic level for the first time. As previously, two subfamilies are recognized, the primitive Ptilocolepinae and the more typical Hydroptilinae, the latter being subdivided provisionally into six tribes, Stactobiini, Leucotrichiini, Ochrotrichiini (new), Neotrichiini, Hydroptilini and Orthotrichiini. Thirteen genera and two species are newly synonymized, three new combinations are established, one previously synonymized genus is reinstated and three genera (*Padunia* Martynov, *Tsukushitrichia* Kobayashi and *Petrotrichia* Ulmer) are transferred to other families of Trichoptera; thus 46 genera with 616 species are considered here as valid

members of the Hydroptilidae. For each genus accounts are given of the nomenclature, distribution, morphology of both adults and immature stages, biology and, where appropriate, species groupings. Keys are given to tribes for adults and to the world genera for both adults and larvae; keys are also provided to differentiate the Ptilocolepinae from the closely related families Rhyacophilidae and Glossosomatidae. The phylogeny of the family is briefly discussed and a synonymic checklist is given of all the species.

Introduction

As a result of a recent investigation into the morphology and biology of the Hydroptilidae, it became apparent that very little was known of the basic systematics of the family. Previous studies on the group have been very fragmentary and have consisted mainly of faunal descriptions and keys, there being no comprehensive appreciation of the family as a whole. The aim of this review has therefore been to investigate the higher classification of the Hydroptilidae with respect to the present knowledge of adult and larval morphology, biology and distribution. Provisional generic keys are given to the adults and to the known larvae, the latter incorporating morphological and case-form data. A full species checklist has also been included which, where possible, indicates tentative species groupings. However, a complete species review was beyond the scope of this work since the family contains over 600 species in 46 genera.

A number of interesting discoveries has been made regarding the systematics and taxonomy of the Hydroptilidae. Fourteen genera and one species have been synonymized for the first time, three species have been transferred to different genera and one genus has been reinstated; three genera have been transferred to other families of Trichoptera. Two subfamilies have been recognized, the primitive Ptilocolepinae and the more typical Hydroptilinae; within the latter six tribes have been provisionally proposed. The Stactobiini is a predominantly Palaearctic group with a small Nearctic component, the larval habits of which are paralleled by the exclusively New World Leucotrichiini. Two other small but distinct Nearctic tribes are the Ochrotrichiini and the Neotrichiini while the remaining assemblage of the generally more successful and more widely distributed genera has been tentatively split into the Hydroptilini and Orthotrichiini.

This revision has been based on the existing literature and on the examination of available adult and immature material. Each genus is separately discussed and data such as distribution, adult and larval diagnostic features, biological details and species groupings are given where possible. Before the detailed systematics are discussed, however, a brief historical review and introduction to the general morphology of the adult and immature stages are given.

Material

Most of the material examined is in the collections of the British Museum (Natural History) (BMNH); additional material was loaned or donated from the collections of the following individuals and institutions.

Higler, L. W. G.	Rijksinstituut voor Natuurbeheer, Leersum, Netherlands
Nybom, O.	Imatra, Finland
Ross, H. H.	Athens, Georgia, U.S.A.
Statzner, B.	Kiel, West Germany
MCM	Merseyside County Museums, Liverpool, England (Dr I. D. Wallace)
UHZIM	Universität Hamburg Zoologisches Institut und Zoologisches Museum, Hamburg, West Germany (Dr H. Weidner, G. Ulmer Collection)
USNM	Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.A. (Dr O. S. Flint, Jr)
ZI	Zoological Institute, Leningrad, U.S.S.R. (Dr L. Zhiltzova, S. I. Lepneva Collection)

Historical review

'Trichoptera in general, but more especially the Hydroptilidae, are an annoyance to the Lepidopterist. If he lives near a river they are a constant source of disappointment to him whenever, on a summer evening, he inspects the entomological miscellany which accumulates upon his tablecloth beneath the gaslight. Down falls a crippled "Micro-"; he has the trouble of looking at it; but his

first glance detects the scabrous clothing of the anterior wings of a Micro-Trichopteron, whose hair looks as if it has been brushed the wrong way, in lieu of the scales of a Micro-Lepidopteron; and his only consolation is that he may leave the pinning of that kind of things to the Trichopterists.'

According to the attitude of most present day entomologists these words could well have been written just yesterday but they were, in fact, part of the introduction to the Reverend A. E. Eaton's paper 'On the Hydroptilidae, a family of the Trichoptera' written over 100 years ago in 1873. Since then the number of described genera and species has gradually increased from 6 and 21 to approximately 50 and 600 respectively but, as stated in the Introduction, little work has been done on the basic systematics of the group and much more material still needs to be collected. It is probably the small size of these insects which is the main deterrent to their collection and identification but, as in all groups, once they are purposefully sought they can be found in quite significant numbers.

The first review of the family was, as already mentioned, that of Eaton (1873) in which he erected four new genera and described six new species. Since then the number of described taxa has steadily increased due to the work of such notable trichopterists as McLachlan, Morton, Mosely and Kimmins in Britain; Ris, Klapálek, Martynov and Schmid on the Continent, and Ross and Flint in the U.S.A. Amongst these, Mosely is perhaps best known for his singular contribution to the description of many new hydroptilid taxa not only from Great Britain and Europe but also many then less well-known regions such as South America, Australia and New Zealand; indeed, according to Kimmins (1951), the family Hydroptilidae was Mosely's favourite group. Kimmins, continuing the work of his predecessor, Mosely, also described a number of new taxa but his most notable contribution was probably his revision of the British species of *Oxyethira* (Kimmins, 1958), a genus with rather complex male and female genitalia, despite which Kimmins succeeded in providing descriptions, figures and keys to both sexes of almost every British representative. Of the Continental contributors, Schmid is perhaps best known for his descriptions of many new exotic genera and species from Sri Lanka, Iran and Pakistan (Schmid, 1958a; 1959b; 1960) and for his review of the genus *Stactobia* (Schmid, 1959a).

Ross, as well as describing many new Nearctic taxa, was the first to break away from the almost classical use of wing venation in the taxonomy of the Hydroptilidae which, due to the small size of these insects, does not provide such reliable characters as it does in the groups of larger caddis flies. Instead Ross employed basic structures of the head, thorax and abdomen which provide more stable features for the differentiation of genera and are also indicative of possible phylogenetic relationships within the Hydroptilidae and between trichopterous families in general. The features thus used by Ross have provided the foundation for the studies outlined in this review. Finally, Flint has made impressive contributions to our knowledge of the Central and South American hydroptilid fauna, especially in his reviews of the Leucotrichiini and the genus *Ochrotrichia* (Flint, 1970; 1972a) and his studies on certain faunal regions such as Jamaica and Surinam (Flint, 1968b; 1974).

The larvae, on the other hand, are less well documented as regards specific descriptions although a significant amount is known at the generic level due to the work of a number of authors of whom special mention should be made of Nielsen. In his monumental work on 'The biology of the Hydroptilidae', Nielsen (1948) describes the morphology, life histories, feeding and case building behaviour of five hydroptilid genera with such detail and accuracy that no subsequent work on this subject has surpassed or even equalled it. Unfortunately it does tend to give rather a restricted impression of hydroptilid larvae in general because it concerns only five of the relatively more advanced and specialized genera and does not stress the diversity of the group as a whole. Nevertheless, it is hoped that this present review will give a much broader appreciation of the family, not only in its immature but also its adult stages, because this cosmopolitan group probably has the greatest ecological, morphological and behavioural diversity within the whole of the order Trichoptera.

Subfamily classification

Stephens (1836) erected the family Hydroptilidae for the genera *Hydroptila* Dalman, *Agraylea*

Curtis and *Narycia* Stephens of which, however, the only species figured, *Narycia elegans* Stephens, subsequently proved to be a tineid moth of the family Psychidae. The Hydroptilidae were basically distinguished from other families of Trichoptera by the unfolded posterior wings and the filiform antennae of the adults and the 'cleft-like' openings of the larval cases. The cases and larvae of *Hydroptila pulchricornis* Pictet and *Oxyethira flavicornis* (Pictet) (as *Hydroptila*) had first been described and illustrated by Pictet (1834) and, in fact, McLachlan (1880) considered Pictet to be the true founder of the family since he had been the first to consider the group as a distinct taxon under the general name of 'les Hydroptiles'.

Nielsen (1948) was the first to attempt to divide the then large and heterogeneous group of hydroptilid genera into subfamilies. Thus Nielsen proposed the Orthotrichiinae for *Orthotrichia* and *Ithytrichia* and the Hydroptilinae for *Agraylea*, *Oxyethira* and *Hydroptila* on the basis of the morphological affinities of the larvae. However, although Nielsen was aware of the other genera known at that time, he only remarked on the relative positions of *Ptilocolepus* and *Stactobia* in his scheme. The subfamily Stactobiinae was erected by Botosaneanu (1956) for *Stactobia* and 'its immediate relatives' which, although not expressly named at the time, probably included *Stactobiella*, *Plethus*, *Plethotrichia*, *Lamonganotrichia* and, possibly, *Catoxyethira*. Ross (1956) proposed a new classification of the Hydroptilidae to include the Ptilocolepinae, a small subfamily consisting of just two small genera with glossosomatid-like adults but typically hydroptilid-like larvae. Ross thus divided the Hydroptilidae into the Ptilocolepinae and the Hydroptilinae, the latter being further subdivided into the Hydroptilini and the Neotrichiini. Flint (1970) subsequently did not adopt Ross's (1956) classification when he proposed the subfamily Leucotrichiinae (later emended to Leucotrichiinae by Flint, *in litt.*) for the Neotropical genus *Leucotrichia* and its related genera, since he retained the Ptilocolepinae, Stactobiinae and Orthotrichiinae as distinct subfamilies. Once again, however, the Hydroptilinae was left as a large and very heterogeneous group; Table 1 shows the two principal approaches to the subfamily classification of the family and compares them with the system to be adopted here. The present views are based on those of Ross (1956) in that only two subfamilies are recognized, with the Hydroptilinae being split into six tribes which correspond to the subfamilies proposed by Flint (1970). These tribes, however, appear to exhibit a number of common features which unite them and distinguish them as a whole from the Ptilocolepinae.

Table 1 Summary of the three views of the subfamily classification of the Hydroptilidae

Nielsen (1948) Botosaneanu (1956) Flint (1970)	Ross (1956)	Proposed classification
PTILOCOLEPINAЕ	PTILOCOLEPINAЕ	PTILOCOLEPINAЕ
STACTOBIINAЕ	HYDROPTILINAЕ	HYDROPTILINAЕ
LEUCOTRICHIIINAЕ	HYDROPTILINI	STACTOBIINI
ORTHOTRICHIIINAЕ		LEUCOTRICHIIINI
HYDROPTILINAЕ		ORTHOTRICHIIINI
		OCHROTRICHIIINI
		HYDROPTILINI
	NEOTRICHIIINI	NEOTRICHIIINI

Systematic position within the Trichoptera

Eaton (1873) first recognized the relationships between adult hydroptilids and rhyacophilids after agreeing with Pictet's (1834) observations that the maxillary palpi of both sexes of the former are five-segmented, thus placing the family in the old subdivision Aequipalpidae (later known as the Aequipalpia). McLachlan retained the Hydroptilidae in the Aequipalpia but, on the basis of the case building habits of the larvae, placed the family between the 'tube-case' building families Sericostomatidae and Leptoceridae. McLachlan also regarded *Ptilocolepus* as a member of the Glossosomatinae ('section II of the Rhyacophilidae') but noted that 'the affinities are certainly

with *Agapetus*' (Glossosomatinae) 'but the thickened erect hairs of the anterior wings show an analogy in the direction of the Hydroptilidae'.

Mosely (1939), on the basis of adult features, considered the family to be closely related to the Rhyacophilidae and had particular difficulty in assigning the Nearctic *Protoptila* group to either one of these families, at first including it in the Hydroptilidae but later transferring it to the Glossosomatinae–Rhyacophilidae (Mosely, 1954) (see discussion on *Padunia*).

Nielsen (1948), using larval and pupal characters, placed the Hydroptilidae between the 'saddle-case' building Glossosomatinae and the 'tube-case' making Integripalpia, the affinities with the latter being particularly evident in the form of the larval antennae and prolegs. Nielsen concluded that the subfamily Hydroptilinae sensu Nielsen (see Table 1) was closest to the Integripalpia, while the Orthotrichiinae sensu Nielsen retained the primitive features of the Rhyacophilidae. Nielsen's views were, however, based entirely on the external morphological features of the larvae which, it should be noted, may be subject to functional modifications correlated with the case building habit. His conclusions regarding the affinities of the Hydroptilinae and the Integripalpia may thus have been influenced by the occurrence of superficially similar characters which have resulted from parallel evolution within the two groups.

Milne & Milne (1939), on the basis of larval anatomy, behaviour and case-form, concluded this of the family: 'the Hydroptilidae is probably more closely related to the Glossosomatinae than the Glossosomatinae to the Rhyacophilidae . . . Hydroptilid larvae being more specialized in the direction of the differentiation of the ends of the case (feeding from one particular end, etc.) than Glossosomatiniids.'

The first serious attempt to construct a phylogenetic classification of the order Trichoptera was made by Ross (1956) who based his conclusions on a comparative study of adult and immature morphology and larval case making behaviour patterns. From this study Ross deduced a set of primitive adult and larval characters and followed the development of these within each group, his findings regarding the evolution of the order being summarized in Chart 1; in this chart the relationships of the Hydroptilidae have been emphasized.

According to Ross (1956), the ancestral caddis fly gave rise to two major evolutionary lines: the 'fixed retreat division', where the larvae simply spin silken nets in which they live and trap their food (the Philopotamidae and the Hydropsychidae–Psychomyiidae complex), and the 'case-maker division', containing all of the remaining families. Within the latter group the most primitive representatives are considered to be the free-living Rhyacophilidae which build stone-covered silken pupal shelters. The early ancestors of the Rhyacophilidae gave rise to the primitive glossosomatid-line, in which the larvae build transportable cases and which in turn gave rise to the more advanced 'saddle-case' building Glossosomatidae and the 'purse-case' building Hydroptilidae. The final step in the evolution of the case building habit was the adoption of the 'tube-case' form as seen in the higher limnephiloid families. Ross considers this major branch to have arisen from the same ancestor as that which gave rise to the hydroptilid line and not from the 'tube-case' building hydroptiline tribe, the Neotrichiini, which would appear to have evolved directly from an early ancestor of the Hydroptilinae. The Ptilocolepinae are considered to be an early offshoot of the hydroptilid line in which many adult features of the more primitive Glossosomatidae have been retained.

In conclusion it would thus seem that the Hydroptilidae may be regarded as a specialized but early offshoot of the case-making branch of the Trichoptera. The family is included in the Rhyacophiloidea, along with the Rhyacophilidae and Glossosomatidae, the other main subdivision being the Limnephiloidea which contains the Limnephilidae, Sericostomatidae and the Leptoceridae. The Hydroptilidae share a common ancestry with the Glossosomatidae with which they have both larval and adult affinities, the latter being most marked in the Ptilocolepinae which also exhibit pupal features intermediate between the Glossosomatidae and the Hydroptilinae. The Hydroptilidae is also regarded as being an early offshoot of the line leading to the Limnephiloidea.

General morphology

Adult

There is a marked difference between the general appearance of the two hydroptilid subfamilies.

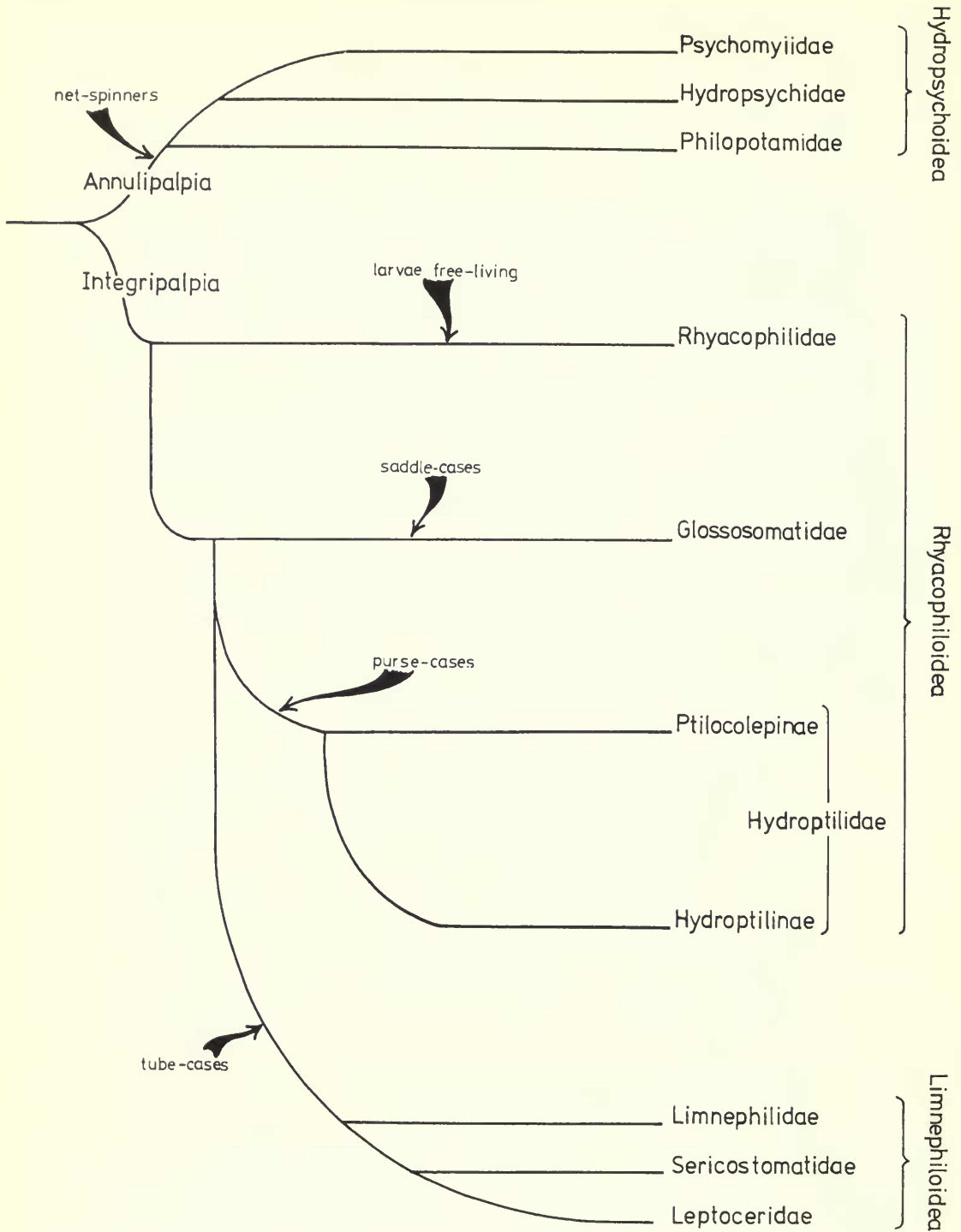


Chart I The position of the Hydroptilidae within the order Trichoptera (after Ross, 1967).



Fig. 1 *Hydroptila tineoides* Dalman, ♂.

The Hydroptilinae have what is normally regarded as the typical hydroptilid form, being small with narrow, pointed wings, long costal fringes, reduced venation and an overall pubescent appearance due to the wings and parts of the body being densely covered in setae (Fig. 1). The Ptilocolepinae, however, look more like small rhyacophilids and glossosomatids, the wings being relatively broad with rounded apices, short costal fringes, an almost full complement of veins (Fig. 5) and a granulose, rather than pubescent appearance due to the presence of sparsely scattered short, unmodified macrotrichia more typical of the order Trichoptera.

The Ptilocolepinae tend to have a rather uniform dark brown to black appearance, reflecting the basic colour of the body, whereas the coloration and markings of the Hydroptilinae are dependent on the arrangement of the setae. These have the same effect, to a certain extent, as the overlapping scales of Lepidoptera and hydroptilids are often mistaken for small moths at first sight, as first noted by Eaton (1873). Hydroptilid setae are usually black, or brown, and white and give the insects a mottled or 'salt and pepper' appearance although, in *Agraylea* for example, this may be partly due to spotting of the wing membrane itself. Distinct metallic hues are seen in some tropical genera and are often caused by the presence of localized groups of modified, scale-like setae.

The Hydroptilidae are described as being small to minute insects and are often termed the 'micro-caddis'. The average forewing length (middle of prothorax to apex of wing) of the Ptilocolepinae is 5 mm (4–6 mm), while that of the Hydroptilinae is 3.5 mm (1.2–6.0 mm). A full account of adult hydroptilids will not be given here; however, those features of taxonomic importance referred to in the systematic section will briefly be described below.

Head capsule

The number of dorsal ocelli varies from the basic complement of 3, to 2 and 0. Posteriorly there is usually a pair of dorsal postoccipital lobes or warts which are somewhat variable in shape, and in the males of the genus *Hydroptila* these are modified as hinged caps which conceal eversible scent dispersing organs lodged in the rear of the head cavity (Fig. 114).

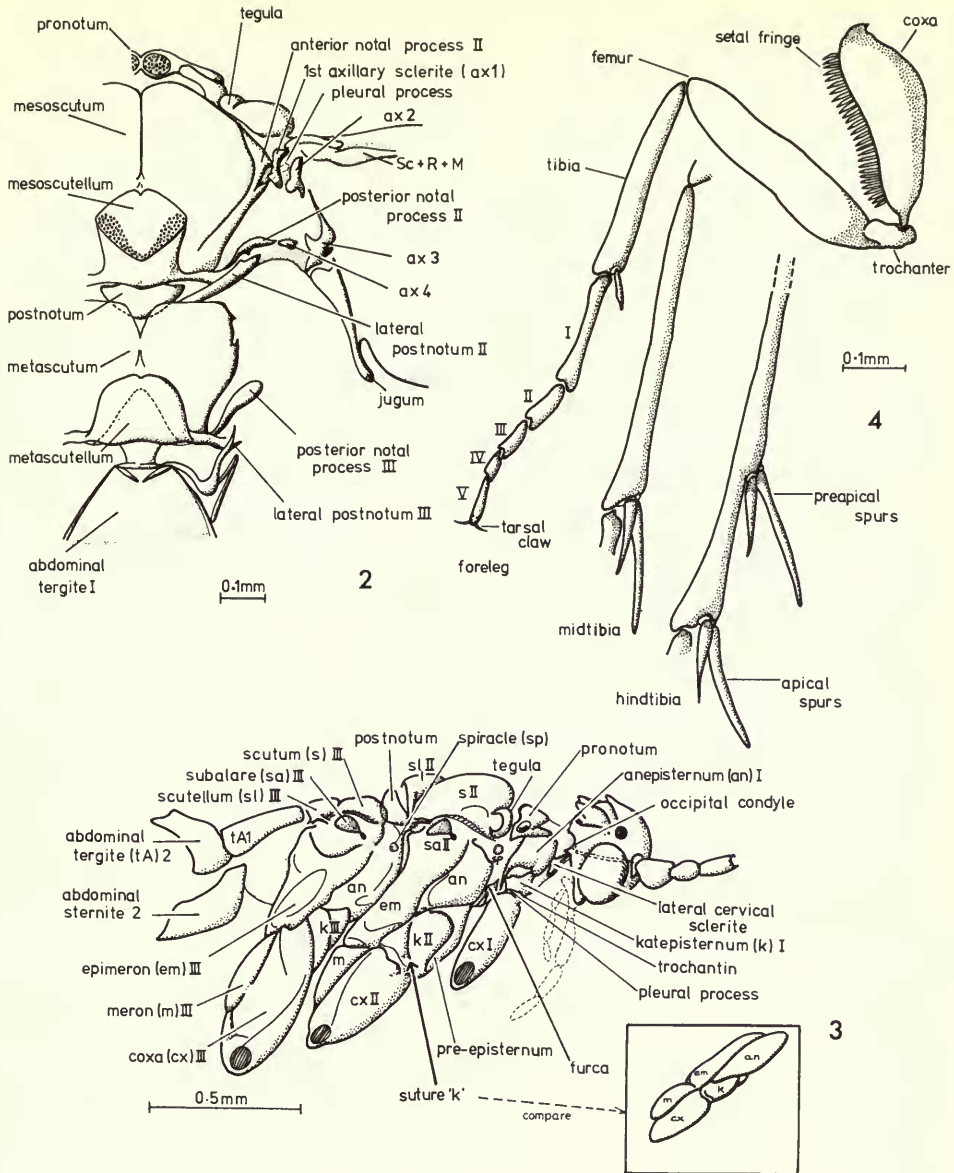
Thorax

The small, ring-like prothorax bears a pair of setigerous protuberances or 'warts' which, in the Hydroptilidae, are characteristically set close together (Figs 53, 62, 83, 108, 114, etc.). The shape of the meso- and metathoracic nota and the presence or absence of transverse sutures provide excellent diagnostic characters at both the subfamily and generic levels; Fig. 2 shows the general terminology employed here. The posterior mesothoracic katepisternal suture (Fig. 3, suture 'k') is characteristically present in the Ptilocolepinae. Ross (1956) first noted the 'general absence' of this suture in the Hydroptilinae (Fig. 3, inset), but I have found this to be a consistent feature of the subfamily. An important feature of hydroptilid taxonomy is the spur formula which refers to the number of tibial spines commonly present on each leg. The maximum number on any one leg is four, consisting of two preapical and two apical spurs; the spur formula gives the number of spines on the fore-, mid- and hindlegs respectively and, for example, in *Stactobia* (Fig. 4) is given as 1.2.4.

The general form of the wings has already been described, the more primitive condition being seen in the Ptilocolepinae (Fig. 5). Here the venation is well developed and resembles that of primitive rhyacophilids (*vide* Ross, 1956 : figs 154, 155) from which it differs in the subcosta (*Sc*) of the forewing and, from rhyacophilids in general, in the fusion of various veins in the hindwing. The Ptilocolepinae differ from the Hydroptilinae in possessing a distinct discoidal cell (*dc*), separate *M*₃ and *M*₄ and a forked *Cu*₁ in the forewing (Fig. 5). The Hydroptilinae are noted for their narrow pubescent wings, reduced venation and long costal fringes (Figs 1, 6–10). In the larger genera, such as *Ugandatrichia* and *Agraylea* (Figs 6, 7), the wings are slightly broader and less pointed apically, the costal fringes are short, the raised setae less dense and the neuration more regular. However, the wings of most hydroptilines are long, slender and highly acuminate. As the overall size of the insect decreases so the wings become reduced and the venation less distinct while the costal fringes become longer to compensate for the loss in wing membrane area. The most extreme examples of wing reduction are seen in *Chrysotrichia* and *Neotrichia* (Fig. 8) (average forewing length 1.5 mm) where the wings are reduced to thin, ribbon-like strips and the venation reduced essentially to the main longitudinal branches *R*, *M* and *Cu*. The compensatory development of the costal fringes parallels the condition seen in other insect groups such as the Thysanoptera, the Trichogrammatidae and Myrmaridae (Hymenoptera) and the Ptiliidae, Clambidae, Corylophidae and some Staphylinidae (Coleoptera). Venational features of the Hydroptilinae do not provide reliable taxonomic characters because, at such reduced dimensions, small variations in crossveins and forks, for example (all of taxonomic importance in the families of larger Trichoptera), are not constant in genera and species of the Hydroptilinae.

Abdomen

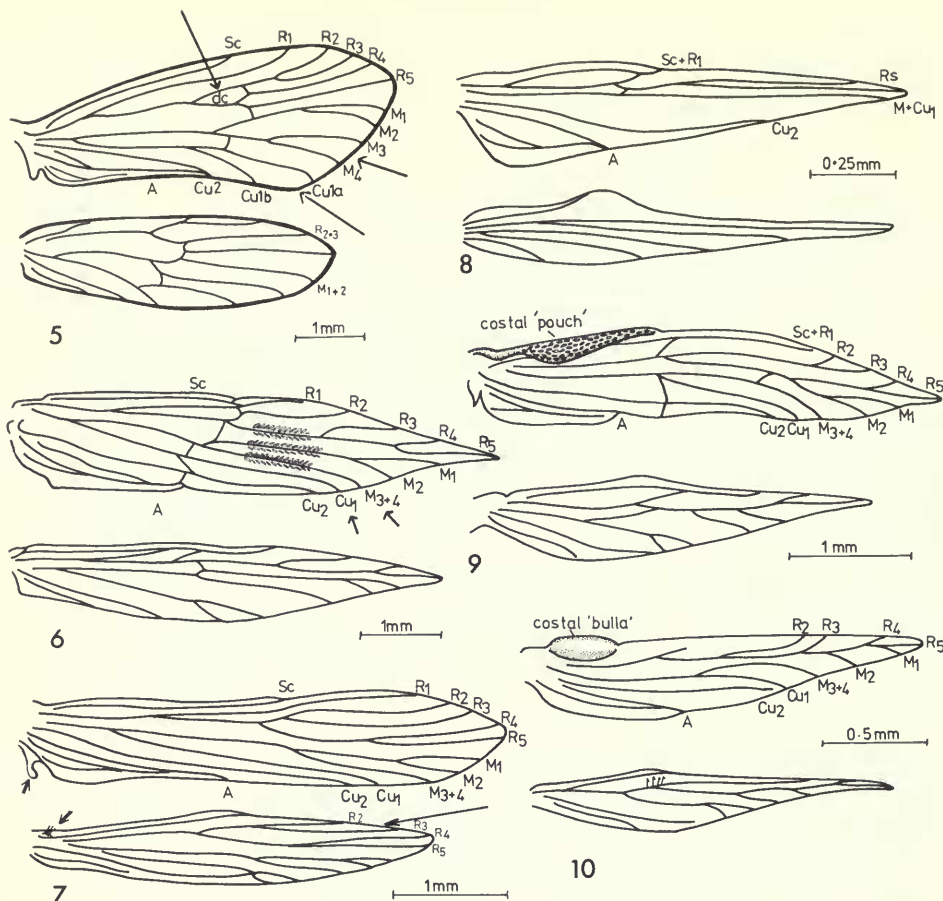
This consists of the usual eleven basic segments (*X* and *XI* being regarded as one) and the sclerites of the posterior segments are modified to form the genitalia. In all hydroptilid genera examined there is a pair of small sternal glands of unknown function which open anterolaterally on the fifth abdominal sternite in both sexes. The external structures associated with these glands differ markedly between the two subfamilies. The Ptilocolepinae again resemble the Rhyacophilidae and Glossosomatidae in having a well-developed sternal ridge (Fig. 11) which, in *Ptilocolepus*,



Figs 2-4 Adult thorax and legs. 2, *Agrylea* sp., thorax and wing base, dorsal view (ax, axillary sclerite); 3, Ptilocolepine, thorax, lateral view (inset, Hydroptilinae, mesopleuro-coxal sclerites); 4, *Stactobia mclachlani* Kimmins, legs and spur formula (1.2.4).

has a pair of long, slender, membranous filaments arising from its anterolateral corners. In the Hydroptilinae there is simply a pair of shallow, subcircular pits in the anterolateral corner of the fifth sternite, from which there also arises a pair of short, posteriorly directed, setate, finger-like processes (Figs 12, 14). *Tricholeiochiton fagesii* (Guinard) is so far unique within the subfamily since there is no process and the surface of the relatively broader pit is irregularly sculptured (Fig. 13). *Ithytrichia lamellaris* (Eaton) (Fig. 14) appears to exhibit an intermediate condition with its reduced process (but relatively elongate seta) and faintly sculptured pit.

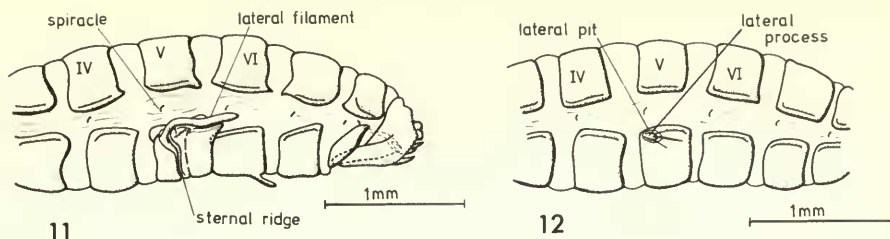
The external genitalia of the Hydroptilidae provide very useful diagnostic characters at both the generic and specific levels. Most species are described from the males only but it has been



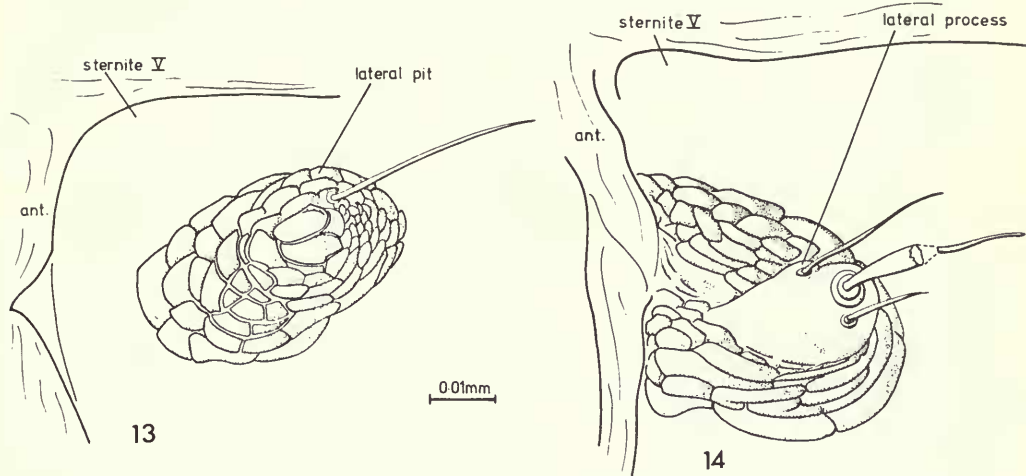
Figs 5–10 Wing venation. 5, *Ptilocolepinae*, *Ptilocolepus granulatus* (Pictet). 6–10, *Hydroptilinae*, (6) *Ugandatrachia cyanotrichia* (Kimmings); (7) *Agraylea* sp.; (8) *Neotrichia anahua* (Mosely); (9) *Abtrichia antennata* Mosely, ♂; (10) *Costatrachia lodora* Mosely, ♂.

found that, if carefully prepared and studied, the female genitalia can also provide useful taxonomic and phylogenetic features. Very little is known of the comparative morphology of hydroptilid genitalia and, as may be expected, authors vary considerably in their terminology of the various structures involved. As a detailed account of hydroptilid genitalia morphology and nomenclature cannot be given here, reference should be made to the generalized diagrams of male and female hydroptilid genitalia (Figs 15–17) which show the terminology to be adopted in this account. However, a short description of the basic features will be given below and a more detailed study of the male genitalia of *Hydroptila occulta* (Eaton), *Agraylea multipunctata* Curtis and *Orthotrichia costalis* (Curtis) is given by Nielsen (1970).

Male. Segment IX forms a distinct genital capsule with a membranous posterior depression (genital chamber) from which arise segment X (the dorsal plate) and the ventral inferior appendages, the aedeagus lying between these two structures. Internal apodemes may arise from the lateral anterior margins (as in the Stactobiini, Figs 65–68) and various external processes may project posteriorly from the anal margin (e.g. *Hydroptila*, Figs 115–117 and *Orthotrichia*, Fig. 135); the latter are termed the side pieces or the lateral or intermediate processes. Segment X is represented by the tergite only and projects from the dorsal posterior margin of segment IX; it is usually entirely membranous, or sometimes weakly sclerotized, and its size and shape vary considerably between taxa. The ventral face of tergite X may fuse with structures ventral to the aedeagus to form a distinct phallic tube, or phallocrypt.



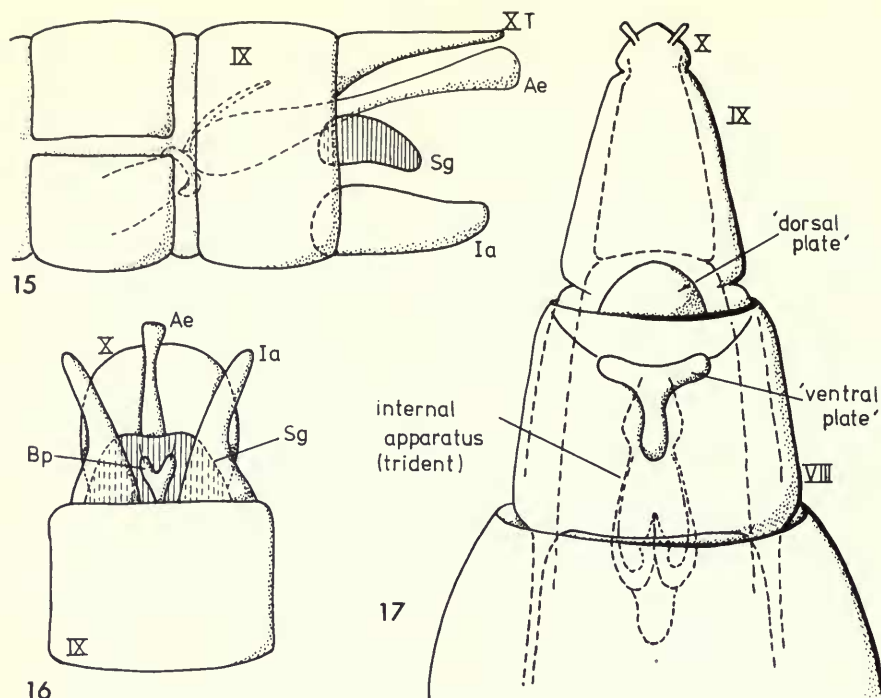
Figs 11-12 Abdomen and sternal gland, lateral view. 11, *Ptilocolepinae* (*Ptilocolepus granulatus* (Pictet)); 12, *Hydroptilinae*, generalized.



Figs 13-14 Sternal gland, abdominal sternite V, antero-dorsal corner, lateral view. 13, *Tricholeiochiton fagesii* (Guinard); 14, *Ithytrichia lamellaris* Eaton.

There has been much confusion over the use of the terms 'superior', 'intermediate' and 'inferior' appendages. True superior appendages, as found in the majority of Trichoptera, are considered by Nielsen (1970) to be absent in the Hydroptilidae; when used in context with this family the term usually refers to a secondarily developed structure. The term 'intermediate' has been variously applied to what has also been referred to as 'superior' and also to what are here called the 'subgenital appendages'. The latter is a non-committal term used to refer to any structure ventral to the aedeagus; when paired they are called appendages (= 'lateral penis-sheaths', 'parameres', 'intermediate appendages') and when fused the structure is termed the 'subgenital plate' (= 'lower penis cover', 'ventral plate of X').

The inferior appendages (gonopods), or 'claspers' as they are usually termed, are one-segmented in the Hydroptilidae as opposed to the two-segmented condition normally found in Trichoptera. They vary considerably in shape, size, additional processes and setae, and provide very useful diagnostic characters at both generic and specific levels (see Figs 55-57, 65-68, 84, 94, 101, 109, 115-117, 122, 129, 131, 135, 140). Ross (1948) introduced the term 'bracteole' for the structure arising from the base of the clasper (Fig. 101), while 'bilobed process' is introduced here to refer to the delicate membranous processes which are seen in a number of genera of the Neotrichiini, Hydroptilini and Orthotrichiini (e.g. Figs 16, 122, 129, 135, *Bp*). The bilobed process usually lies just ventral to the subgenital plate and, although its form is somewhat variable, it consists basically of a pair of short, posteriorly directed processes, each with an apical seta. In *Orthotrichia* (Fig. 135, *Bp*) they may be represented by the single median process formed by the fusion of the paired organs, while in *Oxyethira* (Fig. 122, *Bp*) two pairs of processes would appear to be present which apparently arise from the base of the subgenital plate. It is obvious that much more research into the homologies of hydroptilid genitalia is required.



Figs 15–17 Hydroptilid genitalia, generalized. 15, ♂, lateral view; 16, ♂, ventral view; 17, ♀, ventral view. (Ae, aedeagus; Bp, bilobed process; Ia, inferior appendage; Sg, subgenital process.)

The copulatory organ ('penis', 'phallus') will simply be referred to here as the aedeagus (Figs 15, 16, Ae) as I have made no attempt to homologize the various structures that occur in the Hydroptilidae. The aedeagus is thus basically a long, slender sclerotized tube which, in the Neotrichiini, Hydroptilini and Orthotrichiini (Figs 101, 109, 122, 135, 140, Ae) is distinctly divided into two regions, the proximal, muscular-walled ejaculatory duct and the slender, distal intromittent organ, and also bears a single, spiral 'titillator'. In the other hydroptilid groups where the aedeagus is apparently undivided, the homologies are unknown; each group would appear to have its own specialized structure. In the Stactobiini there is basically a common median duct with a pair of lateral processes which may be variously fused (Figs 69–73). The Leucotrichiini have a very complex structure with 'basal loops' and 'windows' and a membranous apex (Fig. 84) while the Ochrotichiini have an aedeagus which may be very slender (Fig. 94) or heavily spined (Fig. 96). Again, research into the homologies of the hydroptilid aedeagus could prove very rewarding both taxonomically and phylogenetically.

Female. In the Hydroptilidae the female genitalia (Fig. 17) are of the generalized trichopteran condition which is of the simple 'telescopic ovipositor' or 'oviscapt' form (Scudder, 1971). This essentially involves modifications of segments VIII–X and the gonopore is situated ventrally between segments IX and X or, when the sternite IX is reduced as in *Oxyethira* (Fig. 121), apparently just behind segment VIII.

The posterior margin of the ring-like segment VIII bears a number of useful characters such as rows of setae and dorsal and ventral processes and excisions (see Marshall, 1978 for figures of the female genitalia of the British Hydroptilidae). The anterior margin may bear a pair of slender lateral apodemes (Figs 17, 82, 121, 134) and the sternite may have patches of modified setae or, as in *Hydroptila occulta* (Eaton) (Marshall, 1977; 1978), a characteristically shaped sclerite termed the 'ventral plate' by Nielsen (1970) (Fig. 17). The long, slender segment IX forms a retractile 'oviscapt' (Scudder, 1971) or 'false ovipositor' (Nielsen, 1970) which is essentially membranous and has a pair of long, rod-like apodemal sclerites to which the retractile muscles are probably

attached (Fig. 17). Segment IX often bears an anterior ventral sclerite, termed by Nielsen (1970) the 'dorsal plate' (Fig. 17), and the distal end of the segment forms the lower lip of the genital opening. Segment X is greatly reduced and forms the fleshy upper lip of the gonopore; it also bears a pair of short, one-segmented cerci.

In preparations of female abdomens the form of the posterior, partly sclerotized genital ducts ('internal apparatus', Nielsen, 1970) may be more or less discernible, the most noticeable structures being the sclerites of the vaginal wall (Fig. 17). These are what Mosely (1939a) termed the 'trident-like' structures and they are often erroneously referred to as the 'bursa' or 'bursa copulatrix' which are terms indiscriminately used to refer to almost any part of the internal female reproductive system visible in preparations. Such vaginal sclerites, however, along with the dorsal and ventral plates and the posterior margin of segment VIII provide useful specific characters which, I believe, could be put to more use in the future.

The generalized oviscapt form appears to have been modified in certain genera such as *Oxyethira* (Fig. 121) and *Orthotrichia* (Fig. 134) where the genitalia are reduced and specialized in that they are non-retractile and therefore do not have an oviscapt function. Both forms are described in the systematic account and it is possible that their modifications are associated with the oviposition habits of the females which have not, however, been investigated here.

Larva

The family Hydroptilidae is perhaps the most diverse of the Trichoptera with regard to the form of the larvae and their cases since they are structurally adapted to suit a wide range of aquatic environments. The members of the family do, however, share a number of basic morphological and behavioural features which distinguish them from all other Trichoptera and have led to the inclusion of the Ptilocolepinae within the group. Nielsen's (1948) classic work on hydroptilid larvae unfortunately tends to give a restricted view of the family since it deals with only five of the more advanced genera, namely *Agraylea*, *Hydroptila*, *Oxyethira*, *Orthotrichia* and *Ithytrichia* which are all specialized members of the Hydroptilinae. However, Nielsen (1948) does provide an excellent foundation for all studies, whether morphological, biological or behavioural, on the Hydroptilidae and without it the following more general account would have been almost impossible to conceive.

The following account has been based on the literature and on the examination of material in the BMNH or loaned from various institutions. The genera which are known in their larval stages are given below (brackets signify a proposed synonym of the preceding genus; a single asterisk, *, indicates material examined; two asterisks, **, denote a previously undescribed genus).

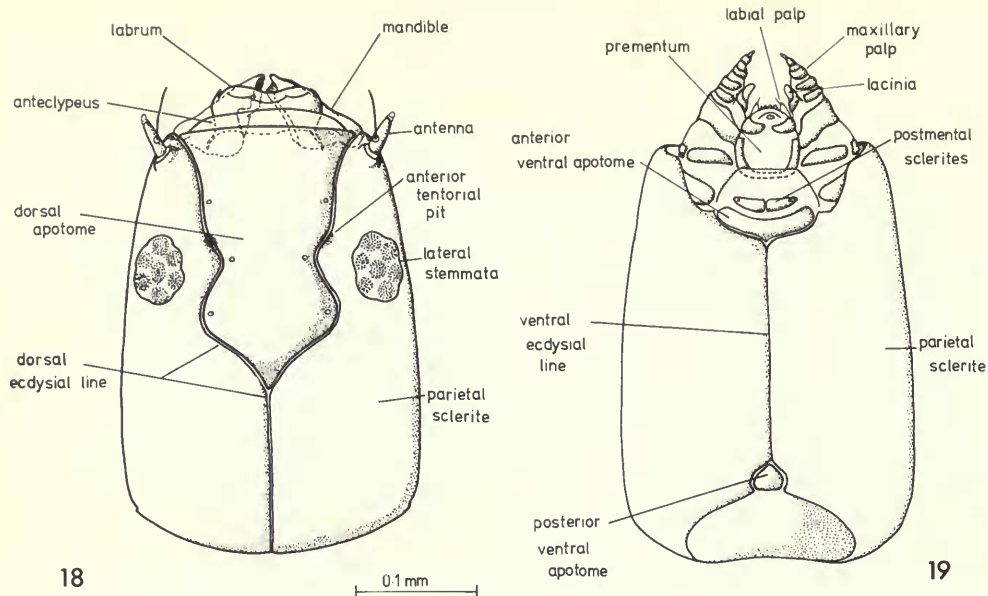
Ptilocolepinae: *Ptilocolepus*, *Palaeagapetus**. Hydroptilinae: *Stactobia**, (*Lamonganotrichia*), *Plethus*, *Stactobiella**, *Catoxyethira*, *Leucotrichia**, *Zumatrichia*, *Peltopsyche*** (previously known from case only), *Anchitrichia*, *Alisotrichia*, *Neotrichia**, *Mayatrichia**, *Agraylea**, *Allo-trichia*, *Ugandatrichia*, *Hydroptila**, (*Oeceotrichia*, *Pasiotrichia*, *Sumatranotrichia*), *Oxyethira**, *Paroxyethira*, *Xuthotrichia*, *Tricholeiochiton**, *Ithytrichia**, (*Sarangano-trichia*), *Orthotrichia**, (*Javanotrichia*, *Baliotrichia*, *Orthotrichiella*), *Dibusa**, *Caledonotrichia***, *Dicaminus* (case only).

A characteristic feature of the family is that the larvae undergo a simple form of hypermetamorphosis in which instars I–IV ('young larvae') are minute, free-living, caseless and of very short duration, while the fifth instar ('old larva') builds a portable or secondarily fixed case and is the principal feeding and growing stage of the life-cycle. The following account of the general external appearance of hydroptilid larvae refers only to the fifth instar; the earlier instars will be discussed later.

General appearance

Despite their case building habits, hydroptilid larvae are prognathous and campodeiform as are the more primitive, free-living and 'saddle-case' bearing groups in comparison with the hypognathous, eruciform, 'tube-case' building limnephiloid groups.

The Hydroptilidae may be distinguished from all other caddis larvae by a combination of the following characters: small size (2.0–7.0 mm body length), enlarged abdomen, three pairs of well-developed thoracic tergites, the absence of segmentally arranged tracheal gills and the fusion of the



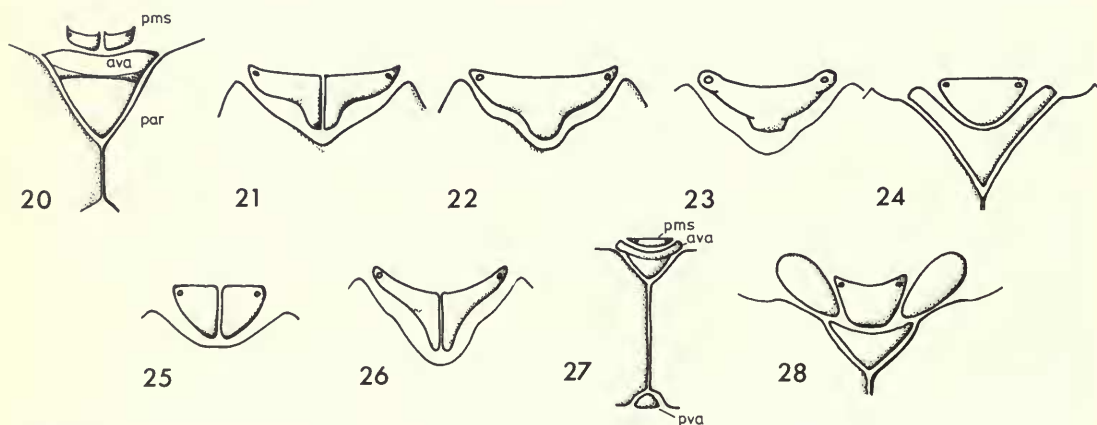
Figs 18–19 Larva, generalized head. 18, dorsal view; 19, ventral view. (Terminology after Hinton, 1963.)

abdominal prolegs to the sides of segment X. The number of abdominal tergites is variable but there is always one on segment IX (the 'anal plate') and in the Hydroptilinae there is usually a pair of small sclerotized (sometimes fused) 'rings' on the terga of segments II/III to VII/VIII.

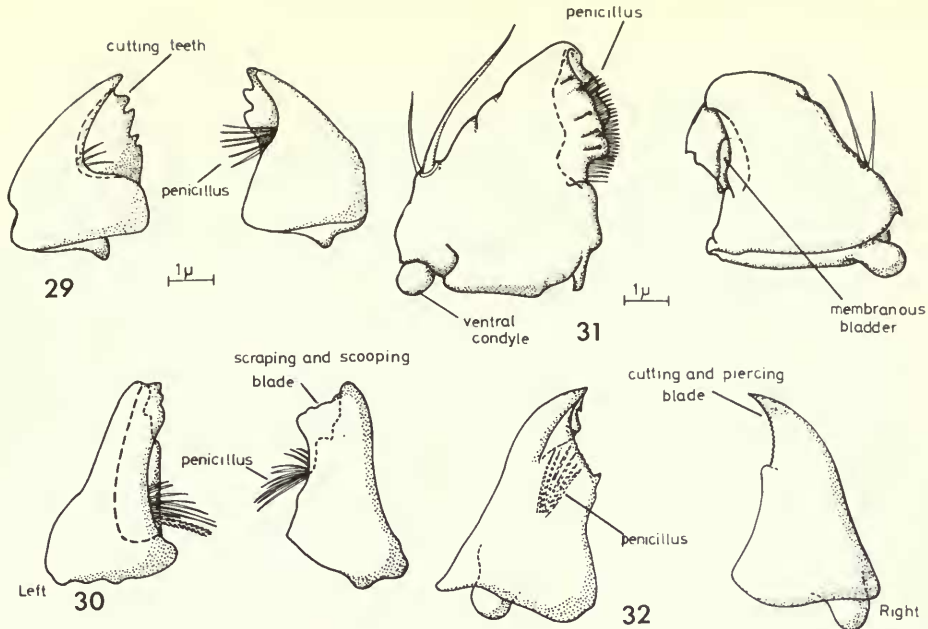
A detailed account of the external morphology of hydroptilid larvae will not be given here; for this, reference should be made to Nielsen (1948). However, features of taxonomic importance or over which there has been some controversy regarding nomenclature will be briefly mentioned below.

Head capsule

There has been some confusion over the homologies of the various regions of the head capsule of trichopteran and endopterygote larvae in general, especially with respect to the ventral sclerites



Figs 20–28 Ventral apotomes and postmental sclerites, larva. 20, *Palaeagapetus celsus* Ross; 21, *Agraylea sexmaculata* Curtis; 22, *A. multipunctata* Curtis; 23, *Tricholeiochiton fagesii* (Guinard); 24, *Ithytrichia lamellaris* Eaton; 25, *Stactobia caspersi* Ulmer; 26, *Hydroptila occulta* (Eaton); 27, *Oxyethira flavicornis* (Pictet); 28, *Orthotrichia costalis* (Curtis). (ava, pva, anterior and posterior ventral apotomes; par, parietal sclerites; pms, postmental sclerites.)



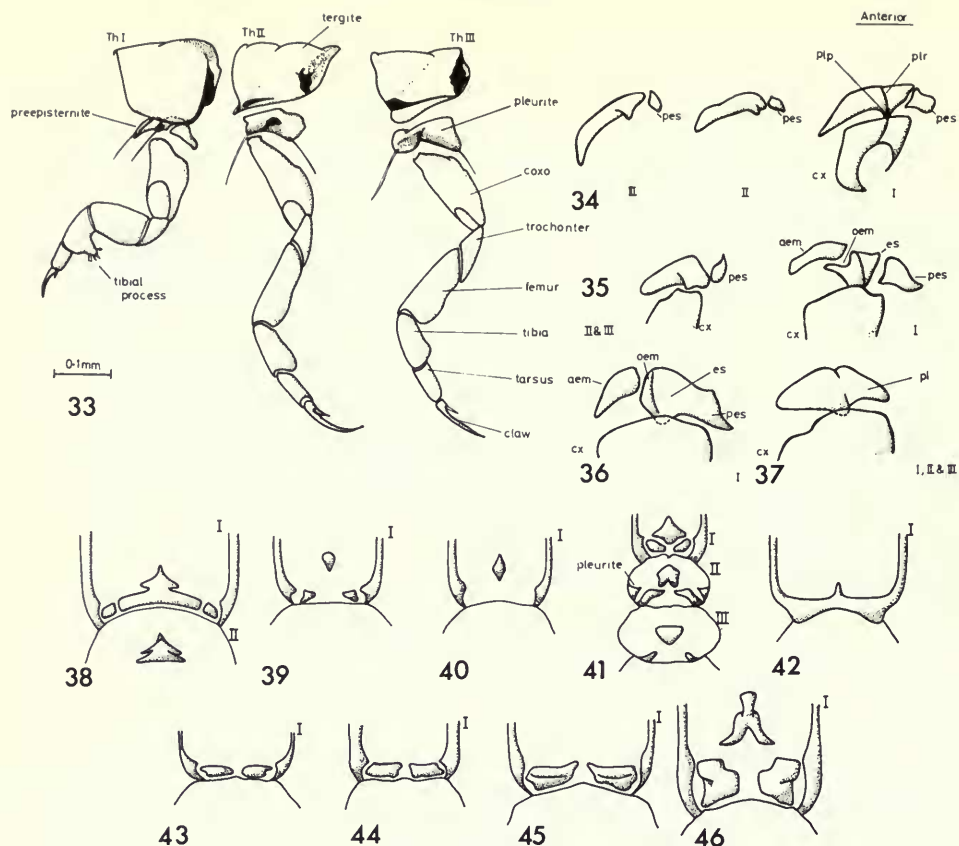
Figs 29–32 Mandibles, larva. 29, *Palaeagapetus celsus* Ross (after Flint, 1962); 30, *Stactobia caspersi* Ulmer (after Botosaneanu, 1956); 31, *Hydroptila occulta* (Eaton); 32, *Orthotrichia costalis* (Curtis) (after Nielsen, 1948).

and the maxillolabial and hypopharyngeal complex. For simplification the terminology proposed by Hinton (1963) has been adopted here and is illustrated in Figs 18, 19. The variety of ventral apotomes and postmental sclerites found within the family is shown in Figs 20–28. The mouth-parts are of the mandibulate type and were probably basically suited for biting through vegetable material as in the Ptilocolepinae (Fig. 29) but, within the Hydroptilinae, two main lines of feeding adaptations may be traced. In the Stactobiini and Leucotrichiini the larvae are primarily detritus-feeding and the mandibles tend to have a form suited to scraping the substrate and scooping up diatoms and other small organic particles (e.g. Fig. 30). In the Hydroptilini and *Orthotrichia*, however, the larvae feed on the fluids of green filamentous algae and the mandibles are adapted for biting or piercing a hole in the cell wall (Figs 31, 32). The mandibles are basically short and robust and one or both may bear a tuft of hair-like spinules (the ‘penicillus’) in the median concavity and which, as in *Hydroptila occulta* (Eaton), for example (Fig. 31), may be replaced in one mandible by a small, membranous ‘bladder’. The form of the mandibles may provide useful generic or specific characters but it should always be borne in mind that such structures may be worn down with age and hence lose some of their external sculpturing.

Thorax

Well-developed tergites are present on all three thoracic segments and each has a distinct mesal suture which, in the prothorax, probably serves as an ecdysial line (Fig. 33). Pleurites are present on all three segments and essentially consist of the fused episternite (*es*) and epimeron (*aem*, *oem*) (collectively termed the ‘pleurite’) separated by the raised pleural ridge (*plr*) which continues ventrally as a short pleural process and articulates with the antero-lateral coxal process (*vide* Fig. 34). A small anterior sclerite derived from the episternite (the preepisternite) may also be present. The various forms of the pleurites found in hydroptilid larvae are shown in Figs 34–37. The thoracic sternites are shown in Figs 38–46.

The thoracic legs of fifth instar hydroptilid larvae are basically of the ambulatorial type which may be modified as short, robust clinging organs in torrenticolous forms (e.g. Fig. 85) or as long, slender appendages in vegetation-dwellers (Figs 123, 132). The general form is shown in Fig. 33,

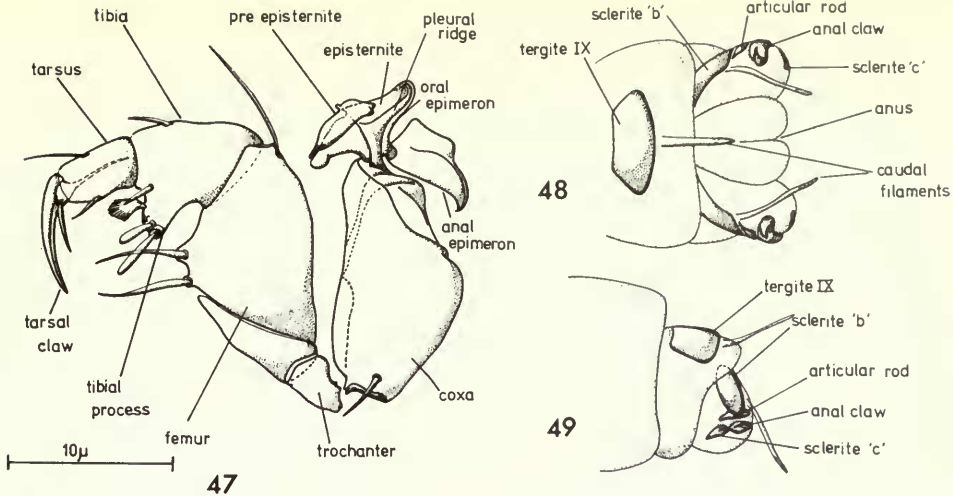


Figs 33–46 Thorax, larva. 33, thorax and legs, *Hydroptila* sp., lateral view. 34–37, thoracic pleurites, lateral view, (34) *Palaeagapetus celsus* Ross; (35) *Agraylea multipunctata* Curtis; (36) *Oxyethira flavicornis* (Pictet); (37) *Dibusa angata* Ross (aem, analepimeron; cx, coxa; es, episternite; oem, oral epimeron; pl, pleurite; plp, pleural process; plr, pleural ridge; pes, preepisternite.) 38–46, thoracic sternites; (38) *Stactobia caspersi* Ulmer; (39) *Hydroptila occulta* (Eaton); (40) *Agraylea multipunctata* Curtis; (41) *Oxyethira flavicornis* (Pictet); (42) *Ithytrichia lamellaris* Eaton; (43) *Plethus* sp.; (44) *Ochrotrichia* sp.; (45) *Caledonotrichia* sp.; (46) *Tricholeiochiton fagesii* (Guinard).

the foreleg always being the shortest and sometimes adapted for special feeding or case-construction purposes. In *Agraylea*, *Oxyethira*, *Paroxyethira* and *Hydroptila* the foreleg (Fig. 47) possesses a distinct modified seta-bearing process against which, according to Nielsen (1948), the tarsal claw may be apposed thus forming a specialized chelate organ used in the manipulation of algal filaments. In general, features of the legs of hydroptilid larvae often provide useful taxonomic characters, especially at the generic level.

Abdomen

In fifth instar, case-bearing hydroptilid larvae, this is uniquely distended in shape and its overall form is usually characteristic for each genus. There are ten distinct segments (XI regarded as being fused with X) which are usually membranous except for the tergite of segment IX; segment X always bears a pair of well-developed anal prolegs which are usually fused to the sides of the segment in case-bearing larvae but project from the sides of the body in free-living forms and in the 'tube-case' building Neotrichiini (Figs 48, 49, cf. 50, 51, 92, 106). In *Hydroptila* and *Ithytrichia* (Figs 48, 49, 118, 141) long filiform caudal filaments are present arising on segments IX and X. Hydroptilinae larvae have dorsal sclerotized rings on abdominal segments II/III to VII/VIII which seem to be a constant feature of the subfamily (Figs 74, 97, 110, 118, 123, 132, 136, 141,



Figs 47–49 Larval thoracic leg and anal prolegs (fifth instar). 47, foreleg and pleurites, *Hydroptila* sp. 48–49, anal prolegs, generalized hydroptilid, (48) dorsal view; (49) lateral view.

143, 147). Nielsen (1948) referred to them as 'dorsal abdominal glands' but they do not appear to have a glandular structure internally and simply appear to be modified epithelial cells. According to Wiggins (1977) they may be regions of specialized chloride epithelial cells adapted for ionic absorption and osmoregulation.

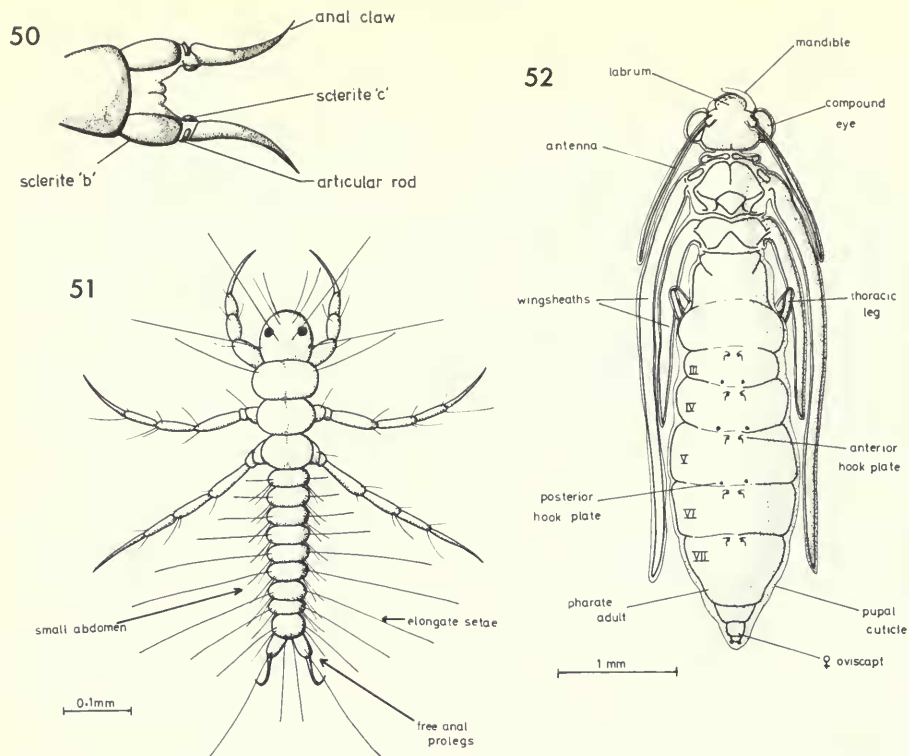
Case

Final instar hydroptilid larvae construct distinctive cases of silk secretion which may be externally sculptured or into which may be incorporated various organic or inorganic particles such as bryophyte fragments, algal filaments and diatoms or small sand grains (which may be added to provide ballast). Ross (1967) coined the term 'purse-case' to distinguish hydroptilid cases from the 'saddle-cases' of the Glossosomatidae and the 'tube-cases' of the higher limnephiloid groups. The 'purse-case' essentially consists of two silken 'valves' closely apposed and joined along the lateral margins (seams) leaving slit-like anterior and posterior openings. It may be laterally (Figs 79, 98, 111, 119, 123, 128, 132, 145) or dorso-ventrally (Fig. 61) compressed and in the latter instance may be temporarily or permanently fixed to the substrate (Figs 75, 76, 78, 81, 86, 148) or it may have a more fusiform shape (Figs 99, 138). As the abdomen of the fifth instar larva increases in size the larva enlarges the case by splitting the dorsal and ventral seams and adding new layers of silk before closing them again (Nielsen, 1948). The Neotrichiini are distinct in having slightly tapering 'tube'-type cases (Figs 103, 107) with circular oral and anal apertures, thus superficially resembling the higher Limnephiloidea. *Alisotrichia* (Leucotrichiini) and *Ugandatrachia* (Hydroptilini) are distinct in that the final instar appears to have lost its case building habit and consequently retains the general appearance of the free-living early instars. The cases of the Hydroptilidae are very distinct for each genus and provide very useful key characters.

The 'young larvae': instars I–IV

Larval hypermetamorphosis is characteristic of the Hydroptilinae, although it has not yet been observed in the Ptilocolepinae, and has so far been recorded in *Agraylea*, *Hydroptila*, *Oxyethira*, *Ithytrichia*, *Orthotrichia* (vide Nielsen, 1948); *Stactobia* (Botosaneanu, 1956; Danecker, 1961; Lepneva, 1964); *Ochrotrichia*, *Mayatrachia* (Ross, 1944), *Paroxyethira* (Leader, 1970) and *Ugandatrachia* (Scott, 1976).

The young larvae are characterized by their relatively smaller size (0.5–2.7 mm, I–early V) and features associated with the absence of a case. They thus have narrow posteriorly tapering abdomens and long, freely projecting anal prolegs while the whole body is covered in long, fine setae



Figs 50–52 Early instars and pupa. 50, anal prolegs, early instar, dorsal view; 51, generalized early instar, dorsal view; 52, pharate adult ('pupa'), *Hydroptila vectis* Curtis, ♀, dorsal view.

which give them the appearance of small, planktonic Crustacea (Fig. 51). The setae offer resistance to sinking and aid the larvae in remaining suspended in the water and in swimming, these instars being the dispersive stages of the larval life-history. In those genera which live in rapids and torrents the larvae are more robust and dorso-ventrally flattened with short legs and few setae, thus being adapted for moving over the surface of the substrate rather than swimming freely. A more detailed account of the early instars is given by Nielsen (1948) who describes both their morphology and their behaviour.

Pupa

The general appearance of the exarate, denticous pupae of most Trichoptera is very uniform throughout the order and the cast pupal skins are difficult to identify beyond the family level. Hydroptilid pupae may be recognized by their lack of any positive distinguishing structural features which variously characterize the other families of Trichoptera. In addition to their relatively small size (1.5–6.0 mm body length), the following features are useful in recognizing hydroptilid pupae (Fig. 52): (i) absence of abdominal gills or lateral lines; (ii) presegmental dorsal abdominal plates on segments III–VII, postsegmental plates on segments III–V; (iii) mandibles symmetrical, short with one or two small median teeth or long or short without teeth or with a fine, serrate cutting edge; (iv) anal seta-bearing processes absent (these only occur in forms where the posterior end of the pupal case is open to admit a water current, the setate processes serving to keep the apertures clear of debris).

Finally, the pupal case generally resembles that of the larva except that the oral and anal apertures are sealed and it is fixed to the substrate. Having attached and sealed the case, the larva then spins the final internal lining and adopts the characteristic prepupal resting attitude in which, according to Barnard (1971), the thorax becomes distended, the abdomen straightens and the

intersegmental grooves become less distinct. According to Nielsen (1948) there is a distinct anterior and posterior differentiation of the larval case and this becomes reversed in the pupal stage. When the pharate pupa is fully developed, ecdysis takes place and the larval exuviae are pushed to the posterior end of the pupal case. The fully developed pharate adult cuts an exit hole in the pupal case and wriggles out with the aid of the dorsal abdominal hook plates. It then makes its way to the surface where it swims around erratically, back uppermost, until it encounters a support on which it climbs out of the water and rests before the final ecdysis.

Systematics

Family HYDROPTILIDAE Stephens

Hydroptilidae Stephens, 1836 : 151. Type-genus: *Hydroptila* Dalman, 1819.

DISTRIBUTION. Cosmopolitan (excluding polar regions).

DIAGNOSIS. *Adult* (Fig. 1) Forewing length 1.2–6.0 mm; forewings moderately to densely pubescent; wings broad with relatively complete venation in the more primitive Ptilocolepinae (Fig. 5) to narrow with highly reduced venation and tapering apices in the more advanced Hydroptilinae (Figs 6–10); ocelli 3, 2 or 0, lateral pair set close to compound eyes some distance posterior to antennal bases; post-occipital warts prominent, meeting postero-medially or represented by loosely hinged sclerites or 'lobes' (Fig. 114); ♀ genitalia usually an oviscap with an elongate telescopic segment IX and a small, cerci-bearing segment X (Fig. 17) (IX rarely reduced and fixed (e.g. Fig. 121)); ♂ inferior appendages one-segmented, genitalia otherwise very variable (generalized plan, Fig. 15).

Larva (e.g. Fig. 118). Campodeiform, prognathous; usually exhibiting hypermetamorphosis; dorsa of all three thoracic segments with paired nota; abdominal gills and lateral line absent; anal prolegs usually fused to sides of segment X in the fifth instar (free in instars I–IV); abdominal tergites present or absent on segments I–VIII, always present on segment IX; dorsa of abdominal segments I–VIII variously with small cuticular rings which may be regions of chloride epithelia; abdomen usually greatly distended in fifth instar; case basically of 'purse-type' (e.g. Fig. 119).

Pupa (Fig. 52). Mandibles usually short with one or two small median teeth (Ptilocolepinae) or with fine serrations along inner edge only (Hydroptilinae); abdominal gills and lateral line absent; apex of abdomen without lobes, processes or specialized cleaning appendages; presegmental hook plates present dorsally on abdominal segments III–VII, postsegmental plates on III–V.

Keys to genera

Adult

- 1 Forewings broad with rounded apices, sparsely pubescent, fringes relatively short; venation well developed, discoidal cell (*dc*) present, *Cu*₁ forked in forewing (Fig. 5); mesonotum convex, prescutum distinct, scutellum subtriangular with a straight posterior margin and a large oval wart (Fig. 53); mesokatepisternal suture (Fig. 3, suture 'k') present; latero-ventral ridge of abdominal sternite V present (with or without a pair of antero-dorsal filaments) (Fig. 11) (Ptilocolepinae) 2
- Forewings narrow, usually acuminate, densely pubescent, fringes long (Fig. 1); venation variable, usually reduced (Figs 6–10), forewing with *Cu*₁ unbranched; mesonotum flat, prescutum absent, scutellum with posterior section forming a flat triangular area with steep sides and a warty texture along edges only (e.g. Figs 62, 114); mesokatepisternal suture absent (Fig. 3, inset); sternite of abdominal segment V with a pair of shallow antero-dorsal pits, each with a short, setae-bearing digitate process (Figs 12–14) (Hydroptilinae) 3
- 2 Veins *R*₂, *R*₃, *M*₁, *M*₂ free in the hindwing; spur formula 2.4.4 (North America; Baltic Amber) *PALAEAGAPETUS* (p. 160)
- Veins *R*₂ + *R*₃, *M*₁ + *M*₂ fused in the hindwing (Fig. 5); spur formula 1.3.4 (Palearctic) *PTILOCOLEPUS* (p. 160)
- 3 Transverse suture present on mesoscutellum (Figs 62, 83, 93) 4
- Transverse suture absent on mesoscutellum (e.g. Figs 108, 114, 120) 20
- 4 Metascutellum subpentagonal to triangular (Figs 83, 93) (Nearctic and Neotropical) 10
- Metascutellum subrectangular to short pentagonal (Palearctic) or as wide as scutum, very short and rectanguloid (Figs 62–64) (Holarctic) 5

- 5 Metascutellum as wide as scutum, short and subrectangular (Fig. 62) 6
 – Metascutellum not as wide as scutum (Figs 63, 64) 8
 6 Spur formula 0.2.4
 (Oriental) *CHRYSOTRICHIA* (p. 170) (Neotropical: Antilles) *BREDINIA* (p. 170)
 – Spur formula 1.3.4 7
 7 ♂ genitalia simple, segment VIII unmodified (Fig. 65) (Holarctic) *STACTOBIELLA* (p. 169)
 – ♂ genitalia very complex, sternite VIII elongate with posterior dorso-lateral spines, segment IX much reduced and withdrawn into VIII (Fig. 68) (Africa) *CATOXYETHIRA* (p. 171)
 8 Spur formula 0.2.3 (SE. Asia) *PLETHUS* (p. 168)
 – Spur formula 1.2.4 9
 9 Fore-tibial spur reduced to a small process; postoccipital lobes narrow, elongate; metascutellum wide, short, rectangular to pentagonal (Fig. 64); ♂ genitalia very complex; ♀ internal apparatus with distinct loop in anterior duct (Fig. 82) (Africa; SE. Asia ?)
 MADIOXYETHIRA (p. 173) (possibly including *PSEUDOXYETHIRA* (p. 174) and *SCELOTRICHIA* (p. 174))
 – Fore-tibial spur unmodified; postoccipital lobes broad, hemispherical; metascutellum narrow, long, rectangular (Fig. 63); ♂ genitalia relatively simple, sternite VIII produced postero-ventrally, IX reduced, VII with elongate process (Fig. 66); ♀ internal apparatus without anterior loop (Palaeartic) *STACTOBIA* (p. 165)
 10 ♂ inferior appendages large and distinct, projecting well beyond segment IX, often armed with various spines and processes (Figs 94–96); head and antennae always simple (Fig. 93) 11
 – ♂ inferior appendages usually short, hardly projecting beyond segment IX (Fig. 84) but if narrow and elongate with elaborate baso-dorsal processes then head and antennae (♂) modified (Figs 90, 91) 13
 11 Fore-tibia without apical spur *OCHROTRICHIA* (*OCHROTRICHIA*) (p. 186)
 – Fore-tibia with apical spur 12
 12 ♂ segment IX produced posteriorly as broad dorso-lateral lobes; inferior appendages narrow, elongate, projecting ventrally just beyond lobes of IX *RHYACOPSYCHE* (p. 187)
 – ♂ segment IX without lateral lobes, inferior appendages broad and elongate, projecting well beyond IX (Fig. 94) *OCHROTRICHIA* (*METRICHIA*) (p. 186)
 13 Spur formula 0.3.4; 0.2.4; 0.2.3; ♂ aedeagus with median constriction only; ♀ tergite VII modified, internal apparatus simple, ring-like *ALISOTRICHIA* (p. 183)
 – Spur formula 1.3.4; ♂ aedeagus with midlength complex (Fig. 84); ♀ tergite VII unmodified, internal apparatus well developed (*Leucotrichia*-group) 14
 14 Basal costal pouch present on ♂ forewing (Figs 9, 10) 15
 – Basal costal pouch absent on ♂ forewing 17
 15 Basal costal pouch large, almost half length of forewing (Fig. 9); head and basal antennal segment (♂) complex (Fig. 91); ocelli 2 (♂) *ABTRICHIA* (p. 183), *Betrichia bispinosa* (p. 182)
 – Basal costal ‘bulla’ small (Fig. 10); head and basal antennal segment (♂) unmodified; ocelli 3 16
 16 Middle antennal segments (♂) wide and flat (Fig. 90). *COSTATRICHIA* (*Iodora*-group) (p. 181)
 – Middle antennal segments (♂) unmodified *ACOSTATRICHIA* (p. 182)
 17 Basal segment of ♂ antenna enlarged *PELTOPSYCHE* (p. 179), *ZUMATRICHIA* (p. 179)
 – Basal segment of ♂ antenna unmodified 18
 18 Ocelli 3 (♂, ♀)
 COSTATRICHIA (*simplex*-group) (p. 181), *Betrichia argentinica* (p. 182),
 LEUCOTRICHIA (*melleopicta*-group) (p. 178) and *CELAENOTRICHIA* (p. 183)
 – Ocelli 2 (♂) 19
 19 ♂ abdominal sternite VIII with postero-lateral processes *ANCHITRICHIA* (p. 181)
 – ♂ abdominal sternite VIII unmodified
 LEUCOTRICHIA (*pictipes*-group) (p. 178) and *BETRICHIA* (partim) (p. 182)
 20 Ocelli absent 21
 – Ocelli present 23
 21 Fore-tibia with apical spur; wings elliptical, ovoid; insect large (forewing length 5.5 mm) (Nearctic) *DIBUSA* (p. 218)
 – Fore-tibia without apical spur; wings acuminate 22
 22 Metascutellum subrectangular (Fig. 133); spur formula 0.3.4; ♂ genitalia markedly asymmetrical (Fig. 135); ♀ genitalia with segment IX relatively short (Fig. 134)
 ORTHOTRICHIA (p. 213)

- Metascutellum pentagonal to triangular; spur formula 0.2.4; ♂ genitalia symmetrical; segment IX of ♀ long, forming an oviscapt; postoccipital lobes of ♂ modified as hinged caps concealing eversible scent organs *HYDROPTILA* (p. 200)
- 23 Mid-tibia with no preapical spur (0.2.3, 0.2.4) 24
- Mid-tibia with preapical spur (1.3.4, 0.3.4) 27
- 24 Spur formula 0.2.3 (Nearctic) *NEOTRICHIA* (p. 189)
- Spur formula 0.2.4 25
- 25 ♂ segment VIII fused, annular; segment IX almost entirely concealed within VIII; forewing length c. 1.6 mm (SE. Asia) *STENOXYETHIRA* (p. 207)
- ♂ genitalia not as above 26
- 26 ♂ segment IX with prominent postero-lateral processes and broad apices; inferior appendages with broad setae-bearing posterior margin and small digitate dorso-lateral basal projection (Nearctic, Neotropical) *MAYATRICHIA* (p. 191)
- ♂ segment IX without processes, inferior appendages apparently absent (Australia) *ORPHNINOTRICHIA* (p. 220)
- 27 Fore-tibia with apical spur (Neotropical: Chile) *NOTHOTRICHIA* (p. 219)
- Fore-tibia without apical spur 28
- 28 Mesoscutellum diamond shaped, narrow (Figs 108, 112, 113) 29
- Mesoscutellum with anterior margin evenly convex, wide (Figs 120, 126, 130, 139) 32
- 29 ♂ ventral process of sternite VII short, laterally compressed, triangular; inferior appendages large, elongate, often broad 30
- ♂ ventral process of sternite VII usually long and spatulate; inferior appendages short and broad, sometimes with short postero-median processes 31
- 30 Lateral filaments of abdominal segment II present in ♂ (India, SE. Asia) *UGANDATRICHIA (MOSELYELLA)* (p. 198)
- Lateral filaments absent (Africa) *UGANDATRICHIA (UGANDATRICHIA)* (p. 198)
- 31 ♂ inferior appendages with concave posterior margins; subgenital plate with a pair of asymmetrical processes bearing asymmetrical spines or filamentous appendages (Fig. 109) *ALLOTTRICHIA* (p. 196)
- ♂ inferior appendages with convex posterior margins (*sexmaculata*-group) or very short with postero-median processes (*multipunctata*-group); processes of subgenital plate absent *AGRAYLEA* (p. 193)
- 32 ♂ abdominal segment VIII fused, annular; segment IX mostly concealed within VIII (Fig. 122); ♀ genitalia not oviscapt, segment IX reduced, tergite usually fused with that of VIII (Fig. 121) *OXYETHIRA* (p. 203)
- ♂ segment VIII with tergite and sternite distinct; ♀ genitalia usually oviscapt 33
- 33 ♂ genitalia very distinctive, sclerites VII and VIII reduced to thin strips, sternite IX enlarged, tergite X forming an elongate narrow plate, inferior appendages short, slender with incurved apices (Sri Lanka) *MACROSTACTOBIA* (p. 217)
- ♂ genitalia not as above 34
- 34 ♂ segment IX with deep dorsal U-shaped incision revealing aedeagus in distinct sheath usually with subapical processes; inferior appendages elongate, concave, broad; ventral processes on segments VII and VIII, latter long and spatulate (Fig. 127) (New Zealand) *PAROXYETHIRA* (p. 208)
- ♂ genitalia not as above 35
- 35 ♂ segment IX produced postero-ventrally (obliquely truncate in lateral view); genital appendages concealed within IX, difficult to homologize (Fig. 131) (NW. Palaearctic, SE. Asia) *TRICHOLEIOCHITON* (p. 210)
- ♂ genitalia not as above 36
- 36 ♂ sternite VI with ventral process; sides of segment IX tapering postero-medially; inferior appendages elongate, parallel, arising near antero-ventral margin of IX, scarcely projecting posteriorly beyond IX (Fig. 140) *ITHYTRICHIA* (p. 216)
- ♂ genitalia not as above 37
- 37 ♂ inferior appendages apparently arising dorso-posteriorly from segment IX, 'bean-shaped' with distinct ventrally directed processes; aedeagus slender, tapering (New Caledonia) *CALEDONOTRICHIA* (p. 221)
- ♂ genitalia not as above 38
- 38 ♂ sternite VII with long, slender process; segment IX with broad postero-lateral truncate side-pieces; aedeagus with distinct apical or sub-apical hook (Fig. 129) (Australia) *XUTHOTRICHIA* (p. 209)

- ♂ genitalia not as above 39
 - 39 ♂ segment IX with postero-lateral side-pieces produced as broad, truncate lobes, segment IX reduced dorsally to thin median transverse strip; aedeagus truncate with well-developed spiral 'titillator' (Yemen, Africa, Zaire) *DHATRICHIA* (p. 199)
 - ♂ segment IX relatively complete dorsally; aedeagus slender with pointed apex or short, spiral 'titillator' (Europe, Pakistan, Aden) *MICROPTILA* (p. 197)
- Larva**
- 1 Small tergites present on abdominal segments I–VIII; larval case dorso-ventrally flattened, fixed to substrate or absent 2
 - Segments I–VIII without distinct tergites; larval case variable but usually not fixed to substrate 9
 - 2 Median sutures of meso- and metathoracic nota indistinct (Nearctic, Neotropical) 6
 - Median sutures of all three thoracic nota distinct 3
 - 3 Fifth instar larva free-living, without case; pupal case sac-like (Africa) *UGANDATRICHIA* (p. 198)
 - Fifth instar larva with distinct case 4
 - 4 Posterior margin of fourth tergite appearing 'crenellated'; case dorso-ventrally flattened, barrel-shaped with mid-dorsal and ventral longitudinal seams (Figs 74, 75) *STACTOBIA* (p. 165)
 - Tergite IX of larva and case not as above 5
 - 5 Case rectangular in dorsal view (Fig. 78) with mid-dorsal and ventral seams; larva (Fig. 77) (SE. Asia) *PLETHUS* (p. 168)
 - Case tapering anteriorly and posteriorly (Fig. 81) without dorsal and ventral seams (Africa) *CATOXYETHIRA* (p. 171)
 - 6 Fifth instar larva free-living, without case; abdomen slender, tapering posteriorly; anal prolegs projecting from sides of abdominal segment X (Fig. 92) *ALISOTRICHIA* (p. 183)
 - Fifth instar in a fixed, oval-circular case, abdomen enlarged, abruptly widened from segments V–VII; anal prolegs fused to sides of segment X 7
 - 7 Anterolateral angle of pronotum produced anteriorly; femora with arborescent setae *ANCHITRICHIA* (p. 181)
 - Anterolateral angle of pronotum not produced; arborescent setae absent 8
 - 8 Tergite IX with short, stout scattered setae (*vide* Figs 87–89) *ZUMATRICHIA* (p. 179), *ABTRICHIA* (p. 183), *PELTOPSYCHE* (p. 179)
 - Tergite IX usually without short, stout setae but if present then in a transverse band (*vide* Figs 85, 86) *LEUCOTRICHIA* (p. 178)
 - 9 Mid- and hindlegs slender, much longer than forelegs 10
 - Thoracic legs short, subequal in length 12
 - 10 Case 'bottle'- or 'jug'-shaped (Figs 123, 124) *OXYETHIRA* (p. 203)
 - Long edges of case almost parallel 11
 - 11 Mid- and hindlegs greater than 4 × forelegs (Fig. 132) *TRICHOLEIOCHITON* (p. 210)
 - Mid- and hindlegs approximately 2.5 × forelegs (Fig. 128) (New Zealand) *PAROXYETHIRA* (p. 208)
 - 12 Abdominal segments with dorsal and ventral 'bud-like' processes; a single filamentous caudal gill present (Fig. 141) *ITHYTRICHIA* (p. 216)
 - Abdominal segments not as above, caudal filaments usually absent 13
 - 13 Abdomen more or less cylindrical; head tapering anteriorly; anal prolegs not fused to sides of segment X; case cylindrical, tapering posteriorly (Nearctic) 14
 - Abdomen flattened dorso-ventrally or -laterally; head not tapering anteriorly; anal prolegs fused to sides of segment X; case flattened with slit-like anterior and posterior openings 15
 - 14 Abdomen slightly depressed, intersegmental grooves prominent; case of secretion and fine sand grains (Figs 102–104). *NEOTRICHIA* (p. 189)
 - Abdomen not depressed, intersegmental grooves indistinct; case of secretion only, surface sculptured usually with transverse or longitudinal ridges (Figs 105–107) *MAYATRICHIA* (p. 191)
 - 15 Labrum with asymmetrical 'beak' (Fig. 137); abdominal segment II with lateral humps (Fig. 136); case fusiform, of secretion only with longitudinal ridges (Fig. 138) *ORTHOTRICHIA* (p. 213)
 - Labrum, abdomen and case not as above 16
 - 16 Tibia of foreleg with pronounced baso-ventral process 17
 - Tibia of foreleg without baso-ventral process 20
 - 17 Abdomen with three filamentous caudal gills; case laterally compressed, of two silken valves covered in fine sand grains and diatoms (Figs 118, 119) *HYDROPTILA* (p. 200)

- Caudal gills absent 18
- 18 Ventral intersegmental grooves of abdomen very pronounced; case of two silken valves covered in radially arranged algal filaments (Figs 110, 111) *AGRAYLEA* (p. 193), *ALLOTRICHIA* ? (p. 196)
- Abdomen and case not as above, exclusively 'New World' 19
- 19 Tarsus with large, plate-like seta and hook claw; antero-lateral expansion of metanotum absent; case fusiform, of secretion only (Figs 99, 100) (Central America) *RHYACOPSYCHE* (p. 187)
- Tarsal seta not plate-like; metanotum with antero-lateral expansion; case usually laterally compressed, of two silken valves covered in fine sand grains, sometimes carried horizontally (dorsal valve vaulted, ventral face flat, of secretion only) (Figs 97, 98) *OCHROTRICHIA* (p. 185)
- 20 Abdomen and case compressed dorso-ventrally 21
- Abdomen and case not compressed dorso-ventrally; tarsal claws stout, abruptly curved with thick blunt spur at base 23
- 21 Case of secretion only with a central tubular section surrounded by lateral fringe, former with a pair of small dorsal pores (Fig. 148; larva, Fig. 147) (New Caledonia) *CALEDONOTRICHIA* (p. 221)
- Case of two silken valves covered in fragments of moss and liverwort (Holarctic, montane regions (*Ptilocolepinae*)) 22
- 22 Abdomen with a pair of lateral tubercles on each segment; abdominal segment I without small tergite (Figs 60, 61) (Holarctic) *PALAEAGAPETUS* (p. 160)
- Abdomen without lateral tubercles; abdominal segment I with small dorsal tergite (Palaeartic) *PTILOCOLEPUS* (p. 160)
- 23 Dorsal abdominal setae stout, dorsal rings of abdominal segments distinct; larva feeding on red algae which are incorporated into silken valves of purse-like case; tarsal claw spurs short, thick and blunt (Figs 143-145) (eastern U.S.A.) *DIBUSA* (p. 218)
- Abdominal setae slender, dorsal ridges indistinct; case of two symmetrical silken valves; tarsal claw spurs elongate, thick, blunt (Figs 79, 80) (Holarctic) *STACTOBIELLA* (p. 169)

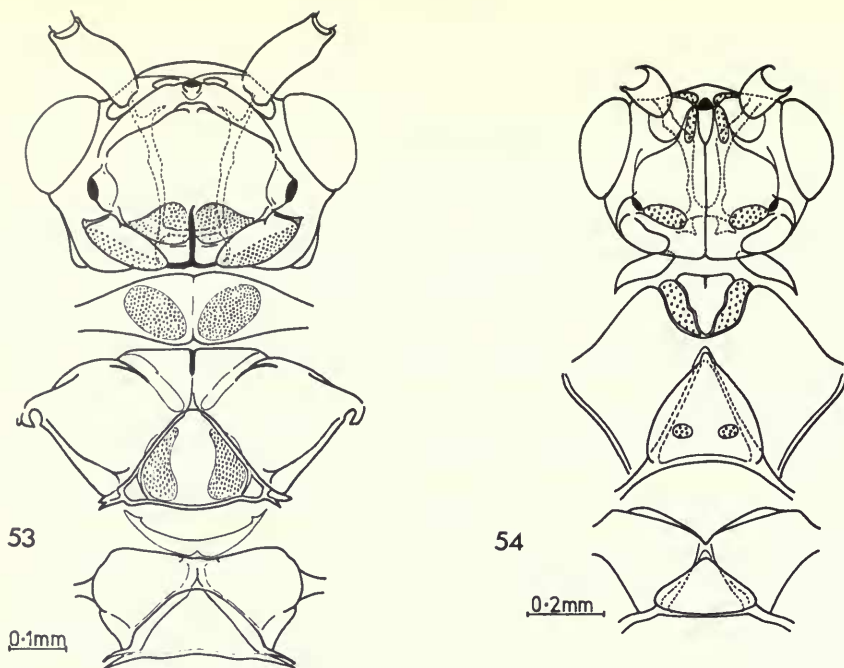
Subfamily **PTILOCOLEPINAE** Martynov

Ptilocolepinae Martynov, 1913a : 22. Type-genus: *Ptilocolepus* Kolenati.

DISTRIBUTION. Holarctic.

The *Ptilocolepinae* contains two small montane genera which are confined to the Holarctic region. *Ptilocolepus*, containing four extant Palaeartic species, and *Palaeagapetus* which is known from the type-species in Baltic Amber and three extant Nearctic species. The adults bear more resemblance to small glossosomatids with which they were once originally classified until discovery of their larval stages indicated that their true affinities were with the Hydroptilidae (Ross, 1956). *Ptilocolepus granulatus* (Pictet) was originally described in *Rhyacophila* but, as Pictet (1834) himself noted, could be distinguished from all other members of the latter genus by its 'rough wings and very ciliated legs'. *Rhyacophila granulata* was later shown to be a senior synonym of *Ptilocolepus turbidus* Kolenati by Hagen (1855), the type-species thus becoming *Ptilocolepus granulatus*. Thienemann (1904) described the larva of *Pt. granulatus* and noted its hydroptilid affinities which prompted Ulmer (1907) to place the genus in the Hydroptilidae. Subsequently, however, Martynov (1913a) erected the *Ptilocolepinae* for the nominate genus but retained it in the *Rhyacophilidae*. It was Ross (1956) who finally transferred the subfamily to the Hydroptilidae, redefining it to include the genus *Palaeagapetus* (earlier in that paper, chart 2, p. 18, Ross refers erroneously to the subfamily as the *Palaeagapetinae*), the inclusion of *Palaeagapetus* later being justified by the discovery of the immature stages of *Palaeagapetus celsus* Ross, described by Flint (1962) and shown to have many affinities with those of *Ptilocolepus granulatus*.

The following subfamily diagnosis is based on the literature and on examination of adult material of *Ptilocolepus granulatus* and *Palaeagapetus celsus* in the BMNH collections and larvae of *P. celsus* loaned from the USNM collection.



Figs 53–54 Adult head and thorax, dorsal view. 53, *Ptilocolepus granulatus* (Pictet); 54, *Agapetus* sp., Glossosomatidae.

DIAGNOSIS. *Adult.* Forewing length 4–6 mm; general body colour dark brown to black, wings somewhat iridescent; wings (Fig. 5) broad with rounded apices, very sparsely pubescent; costal fringes short; venation almost complete, resembling glossosomatid and primitive rhyacophilid conditions in that forewing with discoidal cell (*dc*) closed, *Cu*₁ forked and *Cu*₂ curved: head (Fig. 53, cf. *Agapetus*, Fig. 54) strongly sclerotized, π -shaped tentorium well developed; ocelli 3, lateral pair set close to compound eyes some distance posterior to bases of antennae; antennae short, of approximately 24–30 segments; postoccipital warts large, ovoid, meeting medially; pronotum (Fig. 53, cf. Fig. 54) with median warts close-set; mesonotum strongly convex, prescutum delineated by a row of punctate setal sockets; scutellum subtriangular, convex with a straight posterior margin and a large oval wart; katapisternal suture ('k') present (Fig. 3): metascutellum subtriangular: preapical spur absent from foretibia (spur formula 2.4.4 in *Palaeagapetus* and 1.3.4 in *Ptilocolepus*): abdominal sternite V (Fig. 11) with a well-developed sternal ridge running from anterior dorsal fold, posteriorly and ventrally to meet in midline: ventral processes variously present on sternites VI and VII: ♀ genitalia forming an oviscapt: ♂ genitalia simplified but very specialized within each genus (Figs 55–59) with segment VIII unmodified; segment IX fused, produced antero-ventrally with strongly developed oblique lateral ridges, strongly excised dorsally and ventrally (latter excision containing a triangular ventral plate in *Ptilocolepus* above which lie the fused, generally bifid, 'inferior appendages' (homology uncertain)); 'inferior appendages' apparently fused with segment IX in *Palaeagapetus*; tergite X forming a simple dorsal plate (which in *Ptilocolepus* bears a pair of setose lobes); aedeagus greatly simplified, short, broad and membranous with a dilated apex and a median ventral sclerite.

Larva (Fig. 60). Slightly flattened dorso-ventrally: head with distinct dorsal ecdysial lines; anterior ventral apotome large and triangular, postmental sclerites paired, posterior ventral apotome small and triangular (Fig. 20); labrum symmetrical, anterior margin strongly emarginate with a row of many short setae; mandibles (Fig. 29) not markedly symmetrical, short and stumpy, medial brush present in both right and left, cutting edges strongly ridged: thoracic nota present on all three segments, longitudinal median ecdysial lines distinct on each; thoracic sternites absent; legs short, subequal; preepisternite free on all thoracic segments (Fig. 34); abdomen entirely membranous except for the well-developed tergites of segments I and IX in *Ptilocolepus*; anal prolegs fused to segment X; abdomen with prominent sucker-like tubercles on segments II–VII in *Palaeagapetus*.

Case (Fig. 61). Purse-type, dorso-ventrally compressed (carried horizontally), constructed of two silken valves covered with small fragments of liverwort and moss.

Pupa. Mandibles long with two medial teeth in *Ptilocolepus*, one in *Palaeagapetus*.

BIOLOGY. The larvae occur in small montane springs and seeps, amongst luxuriant growths of moss and liverwort, on stones and other submerged objects; they are often found in the cold damp vegetation above the water level. Habitats in cool, shaded, montane coniferous forests, which favour the growth of bryophytes, are likely to support small colonies of these very local and primitive caddis flies; indeed, McLachlan (1880) noted that the adults of *Ptilocolepus granulatus* were found in European mountainous regions 'on driblets on faces of rocks' where water was soaked up by the moss. The habitat preferences of the Ptilocolepinae are thus very similar to those of the hypothetical ancestral caddis larva as postulated by Ross (1956).

The early stages (instars I–IV) of the Ptilocolepinae have not yet been discovered; the phenomenon of hypermetamorphosis has therefore not been verified in this subfamily.

DISCUSSION. The Ptilocolepinae appear to represent a natural extant link between the primitive Glossosomatidae, with which they share many adult features, and the very specialized Hydroptilinae with which they are classified on the basis of the affinities of the distinctive larvae and their cases. The subfamily is confined to cool Holarctic regions, being found locally in clear, shaded montane springs in association with bryophytes as is typical of the more primitive Trichoptera. The Ptilocolepinae probably thus arose from the main hydroptiline stock very early in the evolution of the family before the typical adult hydroptilid form had been derived. It has since remained very little changed except perhaps with respect to the development of the highly specialized and characteristic male genitalia.

Keys to differentiate the Ptilocolepinae, Glossosomatidae and Rhyacophilidae

Adult

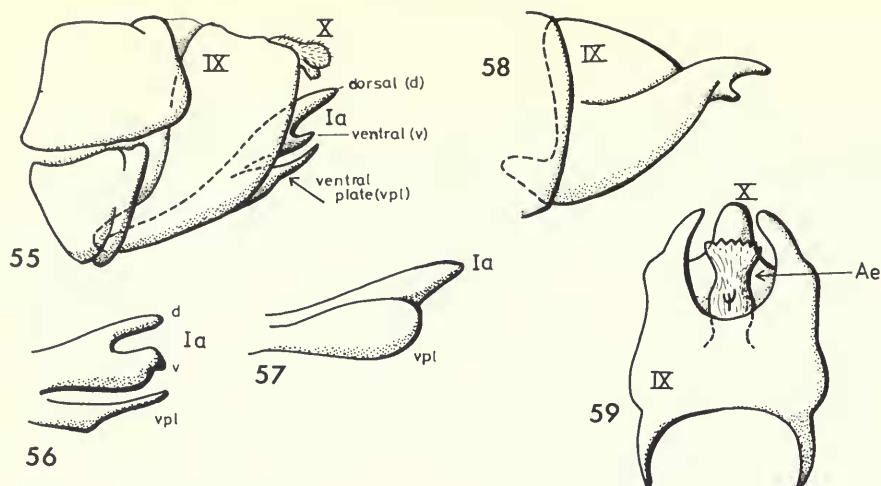
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|---|---|-------------------------------|
| 1 | Discoidal cell of forewing open; spur formula 3.4.4 | RHYACOPHILIDAE |
| – | Discoidal cell of forewing closed (Fig. 5, <i>dc</i>); spur formula 2.4.4 or 1.3.4 | 2 |
| 2 | Spur formula 1.3.4 | PTILOCOLEPUS (p. 160) |
| – | Spur formula 2.4.4 | 3 |
| 3 | Posterior dorsal head warts small, oval or round, widely separated; pronotal warts widely separated (Fig. 54) | GLOSSOSOMATIDAE |
| – | Posterior dorsal head warts large, almost meeting medianly; pronotal warts closely set (cf. Fig. 53) | PALAEAGAPETUS (p. 160) |

Larva (partly after Ross, 1944)

- | | | |
|---|--|------------------------|
| 1 | A pair of well-developed nota present on all three thoracic segments; larvae usually inhabiting purse-type cases of silk with particles of moss and liverwort attached | PTILOCOLEPINAE |
| – | Pronotum only sclerotized; larva without case or with small saddle-like case (flat ventrally, vaulted dorsally) covered in small stones or large sand grains | 2 |
| 2 | Anal prolegs with large elongate hooks; abdominal tracheal gills present or absent; free-living, without case | RHYACOPHILIDAE |
| – | Anal prolegs with very small retractile hooks; tracheal gills absent; with small saddle-like cases covered in small stones | GLOSSOSOMATIDAE |

Pupa

- | | | |
|---|--|-------------------------------|
| 1 | Presegmental and postsegmental dorsal hook plates on abdominal segments III–VII and III–V respectively (Fig. 52) | 2 |
| – | Presegmental and postsegmental hook plates not with full complement as above | 4 |
| 2 | Pupal mandibles without teeth | HYDROPTILINAE |
| – | Pupal mandibles with teeth (Ptilocolepinae) | 3 |
| 3 | Pupal mandibles with 2 teeth | PALAEAGAPETUS (p. 160) |
| – | Pupal mandibles with 1 tooth | PTILOCOLEPUS (p. 160) |
| 4 | Presegmental hook plates always absent from abdominal segment III (i.e. present on IV–VIII; post-: III–IV); spur formula 3.4.4 | RHYACOPHILIDAE |



Figs 55–59 ♂ genitalia, Ptilocolepinae. 55–57, *Ptilocolepus*, lateral view, (55) *Pt. granulatus* (Pictet); (56) *Pt. colchicus* Martynov; (57) *Pt. extensus* McLachlan. 58–59, *Palaeagapetus celsus* Ross, (58) lateral view; (59) ventral view. (vide Figs 15, 16).

- Presegmental hook plates sometimes absent from segment III; postsegmental hook plates always absent from segment III, sometimes also from segment V; spur formula 2.4.4

GLOSSOSOMATIDAE

Genus *PTILOCOLEPUS* Kolenati

Ptilocolepus Kolenati, 1848 : 102. Type-species: *Ptilocolepus turbidus* Kolenati, by monotypy.

DISTRIBUTION. Palaearctic.

Ptilocolepus contains four species which occur in the western Palaearctic region eastwards to the Urals, the Caucasus and Iran, the commonest and most widespread species being *granulatus*. The identity of *villosus* from Spain is questionable due to the inadequacy of the original description (Navás, 1916); the species may prove to be synonymous with either *granulatus* or *extensus* (N.B. *P. villosus* was not referred to by Schmid, 1949, in his paper on the Navás types).

The following key to the males of *colchicus*, *granulatus* and *extensus* is based on a study of material in the BMNH collections. Females of *granulatus* are in the BMNH collections but have not been described; the larva of this species has been described by Thienemann (1904) and Jacquemart & Coineau (1962).

DIAGNOSIS. *Adult*. Branches $R_2 + R_3$ and $M_1 + M_2$ fused in hindwing (Fig. 5), spur formula 1.3.4.

Larva. Abdomen without lateral tubercles, segment I with small dorsal tergite.

Pupa. Mandibles with two medial teeth.

Key to *Ptilocolepus* males (excluding *villosus*)

- 1 Hindwing with patch of modified setae; 'inferior appendages' (Fig. 56, *Ia*) bifurcate with dorsal process not longer than ventral, ventral process broad; 'ventral plate' with process (Fig. 56).
Caucasus and Iran *colchicus*
- Hindwing without patch of modified setae; 'inferior appendages' not as above; 'ventral plate' without process. 2
- 2 'Inferior appendages' (Fig. 55, *Ia*) bifurcate, dorsal process longer than narrow ventral process; 'ventral plate' without process (Fig. 55). Spain, Italy, Central Europe *granulatus*
- 'Inferior appendages' (Fig. 57, *Ia*) non-bifurcate; 'ventral plate' without process (Fig. 57).
Portugal, Spanish Pyrenees. *extensus*

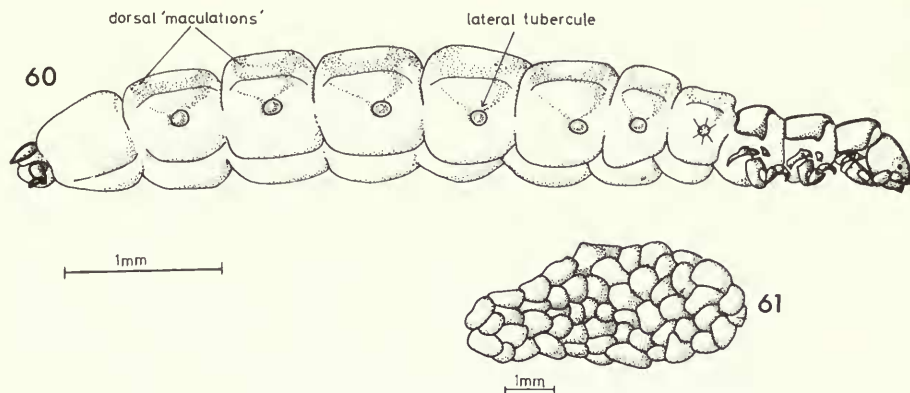
Genus *PALAEAGAPETUS* Ulmer

Palaeagapetus Ulmer, 1912a : 35. Type-species: *Palaeagapetus rotundatus* Ulmer, by monotypy.

DISTRIBUTION. Nearctic (and Baltic Amber).

Palaeagapetus is a small genus containing one fossil species (the type) and three extant Nearctic species. *P. rotundatus* is known only from Baltic Amber and is therefore probably of western European origin (and thus possibly Eocene according to Ross, 1956). The three North American species agree with the type form in features of venation, spur formula and male genitalia. *P. nearcticus* Banks and *guppyi* Schmid are western species, from California to Vancouver Island, while *celsus* Ross occurs in the east from the western Appalachians of North Carolina and Tennessee, New Hampshire to the Laurentians of Quebec (Roy & Harper, 1975). According to Wiggins (1977) it is likely that *celsus* will be found in montane areas between these two extremes.

There is no key to the species of *Palaeagapetus* and only the larva of *celsus* has been described (Flint, 1962).



Figs 60–61 *Palaeagapetus celsus* Ross. 60, larva, lateral view; 61, case, lateral view.

DIAGNOSIS. Adult. Branches R_2 , R_3 and M_1 , M_2 free in the hindwing (cf. Fig. 5); spur formula 2.4.4.

Larva. Abdomen with lateral pairs of segmental tubercles, segment I without tergite (Figs. 60, 61).

Pupa. Mandibles with one medial tooth.

Subfamily HYDROPTILINAE Stephens

Hydroptilidae Stephens, 1836 : 151. Type-genus: *Hydroptila* Dalman, 1819.

DISTRIBUTION. Cosmopolitan (excluding polar regions).

The Hydroptilinae is a very heterogeneous subfamily considered here to contain six distinct tribes characterized by fundamental adult, larval and pupal morphological features which unite them and distinguish them from the Ptilocolepinae.

DIAGNOSIS. Adult (Fig. 1). Forewing length 1.2–6.0 mm: wings narrow with rounded apices and almost complete venation in the larger, more generalized forms (Figs 6, 7) to highly attenuate with consequently reduced venation in the smaller, more specialized groups (Figs 8, 9, 10); Cu_1 unbranched in the forewing (Fig. 6, arrowed); wings densely pubescent, costal fringes usually long and well developed: sclerotization of head capsule reduced in the smaller forms; π -shaped tentorium basically well developed, anterior arms reduced medially to weakly sclerotized filaments (scarcely detectable in KOH-treated specimens) in smaller, specialized genera; ocelli 3, 2 or 0, lateral pair close to eyes and some distance posterior to antennae; antennae usually short, of approximately 30 segments (rarely 40, sometimes 18); postoccipital warts well developed, ovoid to subspherical, often represented by distinct sclerites hinged to the head capsule which, in *Hydroptila* males, conceal eversible scent-organs; compound eyes of variable size but usually occupying whole width of head capsule: thorax (e.g. Fig. 2) with close-set median pronotal warts; mesonotum flat, prescutum absent, scutellum with posterior half forming a triangular flat area with steep sides and a warty texture along edges only, anterior half triangular to arc-like, transverse suture present or absent; mesokatepisternal suture absent (Fig. 3, inset) (I have found this to be a constant feature of the Hydroptilinae, confirming Ross's (1956) view that it is 'usually' absent): fore-tibia with never more than one apical spur; meso-tibia with never more than one preapical spur (Fig. 4): abdomen with ventral processes variable (segments VI, VII or VIII); sternite V (Fig. 12) without postero-lateral ridge but with

a pair of small dorso-anterior pits usually containing a short, posteriorly directed setose membranous process: ♀ genitalia an oviscapt; segment IX usually long and telescopic (Fig. 17), rarely short and fixed with segment VIII modified (Figs 121, 134): ♂ genitalia variable but usually with a characteristic generic or tribe form (generalized form, Figs 15, 16); segment VIII usually with tergite and sternite distinct, rarely fused; segment IX forming an annular 'genital capsule', sometimes with various postero-lateral processes, antero-lateral apodemes and dorsal and ventral excisions, sometimes concealed by segment VIII; inferior appendages (*Ia*) usually present, size and shape variable, sometimes with baso-dorsal processes ('bracteoles'), sometimes fused and at times withdrawn into segment IX; tergite X reduced to dorsal plate (may be absent), size and degree of sclerotization variable; subgenital plate (process) or appendages (*Sp*) present; bilobed process (*Bp*) present ventral to subgenital plate, consisting of a membranous process with two short apical setae (sometimes appears to be fused to subgenital plate); aedeagus (*Ae*) variable but basically a long narrow sclerotized tube enclosing the phallosome which opens apically, a pair of lateral processes may occur along apical half (sometimes fused together or with central tube) which may be represented by a single spiral 'titillator' (homologies uncertain).

Larva. Early instars (I–IV) free-living (Fig. 51), fifth instar case-bearing (e.g. Figs 74, 75). All three thoracic segments with paired nota completely covering dorsa; abdomen distended, membranous, compressed laterally or dorso-ventrally, rarely cylindrical, abdominal gills absent. Ecdysial lines of head distinct (Figs 18–19), sometimes fused; ventral apotome and postmental sclerites variable (Figs 21–28), small posterior ventral apotome sometimes present (Fig. 27); labrum basically symmetrical; mandibles (Figs 30–32) primitively symmetrical and each with mesal brush (in left mandible only in specialized groups), cutting edges ridged or modified as sharp blades or 'scoops' (Figs 31–32); thoracic sternites variable (Figs 38–46) with a maximum of three per segment (one median 'oral' and two lateral 'anal'); pleurites primitively with preepisternite free on all segments, usually free on segment I only; anal epimeral pleurite sometimes present (Figs 35–37); legs variable, basically short and subequal, modified variously as robust, strongly clawed clinging organs (e.g. Fig. 89) or with mid- and hindlegs long and slender as in vegetation dwellers (e.g. Figs 123, 128, 132); abdominal tergites present or absent, tergite IX always present; dorsal 'rings' usually present on segments I/II–VIII; anal prolegs usually fused to sides of segment X (except in early instars and fifth instar of *Alisotrichia* and the *Neotrichiini*).

Case. Variable, basically purse-like of two silken valves with anterior and posterior slit-like openings (e.g. Fig. 119), sometimes with incorporated inorganic or organic particles; usually held horizontally. Sometimes, however, the case may be cylindrical or fusiform with slit-like (Fig. 138) or circular (Figs 103, 107) openings; in specialized torrenticolous or madicolous forms the case is greatly flattened dorso-ventrally and firmly fixed (temporarily or permanently) to the substrate (Figs 75, 78, 86) and may sometimes have lateral 'wings' (Figs 76, 81, 148).

Pupa. Of the typical hydroptilid form (Fig. 52); presegmental and postsegmental plates on abdominal dorsa III–VII and III–V respectively; mandibles without teeth, usually long. Case formed by sealing the larval case which has been previously attached to the substrate by adhesive discs at the corners or by one seam.

BIOLOGY. The subfamily contains both cool- and warm-adapted genera which occur in a wide variety of habitats; it is almost cosmopolitan in distribution, being absent only from the extreme polar regions. Habitat preferences range from seeps, springs and splash zones of waterfalls to clear, fast-flowing montane streams, and from all sizes of rivers to still (but rarely stagnant) ponds in lowland regions.

The larvae are basically detritus-feeders but some groups have adopted special methods for feeding on the fluid contents of the cells of filamentous green algae, the most specialized genus in this respect being *Orthotrichia*. The distribution and life-histories of the algal-feeding groups are dependent on those of the algae, and genera vary as to whether they occur with the algae on the substrate or amongst vegetation. The primitive Nearctic genus *Dibusa* is unique in that it is associated with the red fresh-water alga, *Lemanea* (Wiggins, 1977).

Key to tribes (for keys to genera see p. 153)

Adult

- | | | |
|---|---|--------------------------------|
| 1 | Transverse suture present on mesoscutellum (Figs 62, 83, 93) | 2 |
| – | Transverse suture absent from mesoscutellum (e.g. Figs 108, 114, 120) | 3 |
| 2 | Metascutellum subpentagonal to triangular (Figs 83, 93) (Nearctic, Neotropical) | |
| | | LEUCOTRICHIINI (p. 175) |
| – | Metascutellum subrectangular to short pentagonal (Palearctic) or as wide as scutum, very short and rectanguloid (Figs 62–64) (Holarctic, Palaetropical) | STACTOBIINI (p. 163) |

- 3 ♂ aedeagus thread-like or armed with thickened spines, spiral 'titillator' absent (Figs 94, 96) (Nearctic) OCHROTRICHIINI (p. 184)
- ♂ aedeagus usually divided into proximal and distal sections, spiral 'titillator' usually present (Figs 15, 101, 109, 122, 135, 140) 4
- 4 ♂ genitalia asymmetrical (Fig. 135) or with segments IX and X membranous dorsally, IX incomplete ventrally with lateral sides tapering posteriorly, inferior appendages slender (Fig. 140) (cosmopolitan) ORTHOTRICHIINI (p. 212)
- ♂ genitalia symmetrical, not as above 5
- 5 Adults small, forewing length 1.5–2.0 mm; segment IX or inferior appendages of ♂ genitalia with a pair of broad, flat, spatulate processes or lobes (bracteoles) (Fig. 101) (Nearctic, Neotropical) NEOTRICHIINI (p. 188)
- Adults small to large, forewing length 1.5–6.0 mm; ♂ genitalia very variable, usually without broad bracteoles (Figs 109, 115–117, 122, 127, 129, 131) (cosmopolitan) HYDROPTILINI (p. 191)

Tribe STACTOBIINI Botosaneanu stat. n.

Stactobiinae Botosaneanu, 1956 : 382. Type-genus: *Stactobia* McLachlan, 1880.

DISTRIBUTION. Holarctic.

Botosaneanu (1956) erected the subfamily Stactobiinae for *Stactobia* and 'les genres étroitement apparentes' (*Stactobiella*, etc.). Although Botosaneanu did not name these genera, he probably intended the group to include *Stactobiella*, *Plethus*, *Plethotrichia* and *Lamonganotrichia* as suggested by the knowledge of the group at that time. Ulmer (1957) considered *Plethus* and *Lamonganotrichia* to be closely related according to their larval affinities; on adult features alone, however, *Plethus* bears more resemblance to *Plethotrichia* while *Lamonganotrichia* is more like *Orthotrichia*. Ulmer also considered the larva of *Plethotrichia* to have more affinity with that of *Hydroptila* and consequently placed it in the Hydroptilinae sensu Nielsen (1948) (*vide* Table 1).

Schmid (1959a), despite recognizing Botosaneanu's subfamily grouping, remarked on the relationships of *Stactobia* with *Stactobiella*, *Chrysotrichia*, *Madioxyethira*, *Pseudoxyethira*, *Parastactobia*, *Macrostactobia* and *Plethus* (the last of which Schmid considered *Plethotrichia* to be a possible synonym). Flint (1970), on the basis of larval morphology and case form, considered *Plethus* and *Lamonganotrichia* to belong in the Stactobiinae but placed *Stactobiella* in the Hydroptilinae sensu Nielsen (1948) along with *Hydroptila*, *Agraylea* and *Oxyethira*.

Morse (1974) has independently remarked on the relationship of *Catoxyethira veruta* Morse, from S. Rhodesia, with the Holarctic genus *Stactobiella* according to features of the adults; Ulmer (1957) had previously noticed the relationship of the larvae of *Catoxyethira* and *Stactobia*.

Examination of adult type-material has revealed errors in the original diagnoses of the genera which are henceforth considered to comprise the tribe Stactobiini; such anomalies have occurred in the interpretation of spur formulae, presence of ocelli and wing venation features, all of which were once considered to be very important in deducing generic relationships. The present grouping is thus based on more reliable features such as the male and female genitalia, head and thoracic structures and amended ocellar counts and spur formulae; a number of previously unsuspected relationships and possible synonymies have also been discovered.

Since the constituent genera exhibit a number of larval and adult features which are unique to the stactobiines the group is treated as a distinct tribe although three main genus-groups may be recognized. These are the *Stactobia*-group (*Stactobia* and *Plethus*), the *Stactobiella*-group (*Stactobiella*, *Bredinia*, *Parastactobia* and *Chrysotrichia*) and the *Madioxyethira*-group (*Madioxyethira*, *Pseudoxyethira* and *Scelotrichia*). Within the tribe the genera show various lines of development and specialization in either the larval or the adult stages or both, but they all share the basic common features (set out below) from which the principal characters of a hypothetical stactobiine ancestor may be deduced. As more becomes known of the group, especially of the larval stages, the following tentative conclusions may accordingly require modification.

DIAGNOSIS. *Adult* (Figs 62–64). Head with tentorium complete; antennae short, usually 18-segmented; ocelli 3: mesoscutellum with transverse suture; metascutellum with anterior edge approximately straight, parallel with posterior edge; abdominal segment V with typical short, lateral setose processes: ♀ genitalia

an oviscap: ♂ genitalia (Figs 65–68) with tergite and sternite VIII distinct; IX reduced ventrally, sternite vestigial (absent or fused with tergite ?); inferior appendages small, distinct; paired subgenital structures ('subgenital appendages', Schmid, 1959a) heavily sclerotized, arched downwards, sometimes represented by a fused sclerite (?); bilobed process absent; tergite X absent or reduced; aedeagus (Figs 69–73) long, straight, without median constriction or spiral titillator, basically tripartite with a single apical process arising midlength beneath (or above) which are two flattened processes fused along most of their length (often only the apex reflects this form as a dilated, trilobed structure), sometimes rows of short apical setae or heavily sclerotized subapical spines may be present.

Larva. The larval stages are only known for *Stactobia*, *Plethus*, *Stactobiella* and *Catoxyethira* (including also *Lamonganotrichia* and *Plethotrichia*). The genera have different structural adaptations associated with their various habits and ecological preferences and do not appear superficially to be as homogeneous as the adults. The generalized larval form, as seen in *Stactobiella*, is that of the typical hydroptilid with the fifth instars inhabiting transportable purse-type cases. However, the main evolutionary trend within the group has been the adaptation to life in fast-running water and the thin surface film of water on rocks (the madicolous, hygropetric or hydropetric habitat). Various degrees of specialization occur but the basic trends are towards the dorso-ventral flattening of the body and case, the attachment of the case to the substrate, the protection of the body by fusion and thickening of dorsal sclerites and the development of the thoracic legs as strong clinging appendages. The most advanced genus in this respect is *Stactobia*, which is truly madicolous, while *Plethus*, according to Schmid (1958a), although morphologically similar to *Stactobia* does not share its 'hydropetric' habits. Schmid (1960) also states that *Madioxyethira milinda* is exclusively madicolous, but this is purely speculative since the larva of this species is unknown.

Pupa. Typically hydroptilid with no distinguishing characters; mandibles long, without teeth.

DISCUSSION. On the basis of adult and, to a lesser extent, larval affinities the genera of the Stactobiini as defined here appear to fall into three natural groups. Each group contains both generalized and highly specialized representatives of which the former exhibit the basic features by which the relationships of the three groups may be recognized.

The *Stactobia*-group is distinguished by the shape of the metascutellum and the general form of the larvae. *Plethus* would appear to be the most typical and generalized representative on account of the unmodified male genitalia, which are highly specialized in *Stactobia*, and the larvae which, although obviously adapted for life in running water, are not, according to Schmid (1958a), as hygropetric in their habits as are those of *Stactobia*. *Plethus* is restricted to the SE. Asian region while *Stactobia* appears to be a more successful group with a continuous recent temperate distribution in the Old World and a few subtropical representatives. The *Stactobia*-group appears to fill the Old World niche occupied by the Leucotrichiini in the New World. *Lamonganotrichia* is grouped with *Stactobia* and *Plethus* on the basis of larval affinities whereas *Plethotrichia*, although almost identical with *Plethus* in male genitalic features, most closely resembles *Stactobiella* in larval features; the latter may simply be due, however, to the retention of the generalized hydroptilid form in both these genera.

The *Stactobiella*-group is characterized by the distinctive narrow, strip-like form of the metascutellum of the adults. *Stactobiella*, *Bredinia* and *Chrysotrichia* have generalized male genitalia very similar to those of *Plethus*; *Catoxyethira* and *Parastactobia*, however, both have very unusual, specialized genitalia. The group as a whole has a wide distribution with Palaearctic, Nearctic, Oriental and African representatives. Only the larval stages of two genera are known, *Stactobiella* from a single Nearctic species (which has the unmodified hydroptilid form) and *Catoxyethira* from essentially an unidentified African species which, according to Ulmer (1912b; 1957), resembles that of *Stactobia*. It may thus be that the larvae of *Stactobiella* (and *Plethotrichia*) have retained the basic hydroptilid form while those of *Stactobia* (including *Lamonganotrichia*), *Plethus* and *Catoxyethira* have become adapted and structurally modified for life in fast-running water conditions.

Madioxyethira, *Pseudoxyethira* and *Scelotrichia* are African and SE. Asian genera grouped here according to the shape of the mesoscutellum, the reduced apical process of the fore-tibia, the shape of the post-occipital lobes and the unique forms of the male genitalia (and possibly also the genital-duct loop of the female). The larvae of these genera are completely unknown but they are included in the Stactobiini on the basis of the form of the thorax and the short antennae, and because the male genitalia may be derived from the basic stactobiine form.

It would thus appear that the Stactobiini is essentially an early offshoot of the main Hydroptilinae branch with representatives which have become isolated in the now equatorial regions of Africa and SE. Asia. *Stactobiella* is distinct in that it has a more northerly Holarctic distribution with local species in montane habitats extending from Central Europe to the eastern United States. The most successful and best represented genus is *Stactobia*. This may be due to its specialized larval habits which allow it to fill a unique niche with no competition from any other Palaearctic hydroptilid. *Stactobia* also has a continuous Palaearctic distribution.

The Stactobiini may have arisen from originally 'cool-adapted' montane stream-dwelling ancestors which gave rise to two main lines, the first (1) becoming 'cool-temperate-adapted' while the second (2) became more 'warm-adapted'. Line 1 is the *Stactobiella*-group containing the 'cool-adapted' genus *Stactobiella* which has retained a northerly distribution. It appears to have crossed via the Bering route down into the North American mountain chains of the western 'Rockies' and eastern Laurentians and Appalachians, where isolated populations are still maintained. A more 'temperate-adapted' line leading to the African and SE. Asian genera *Chrysotrichia*, *Catoxyethira* and *Parastactobia* may also have arisen from line 1. The North American *Stactobiella* line may have given rise to (if *Stactobiella* is not synonymous with) the Central American genus *Bredinia*.

Line 2, consisting of the *Stactobia*- and *Madioxyethira*-groups, became more 'warm-adapted' and probably had a past continuous distribution extending from Africa through North Africa, SW. Asia to SE. Asia at a time when these areas were linked by one great forest. When the climate became drier and severed the links between these two continents, representatives of these once widespread genera became isolated in the Oriental and African regions where the original conditions were, and still are, maintained. In the latter continent these areas occur in the forests surviving in western Africa, the mountain slopes of eastern Africa and along the rivers through to southern Africa which are precisely the regions from which these hydroptilids have been recorded, namely Nigeria and Zaire (compare also the distribution of *Ugandatrichia*). The most recent successful representative of line 2, *Stactobia*, now has a continuous subtropical Palaearctic distribution in the mountain ranges extending from eastern Asia (Japan) through Asia Minor, the Mediterranean region and North Africa out to the Atlantic Islands. Some species of the *furcata*-group have spread northwards into the more temperate Central European regions while representatives of the *vaillanti*-group have been discovered in Africa (Guinea and Uganda).

In conclusion, the Stactobiini appears to have arisen from an ancestor which evolved early in the history of the Hydroptilinae. The tribe is quite distinct from any other belonging to this subfamily and its possible relationships with the New World tribe Leucotrichiini will be discussed later.

Genus *STACTOBIA* McLachlan

Stactobia McLachlan, 1880 : 505. Type-species: *Hydroptila fuscicornis* Schneider, by subsequent designation by Mosely (1933).

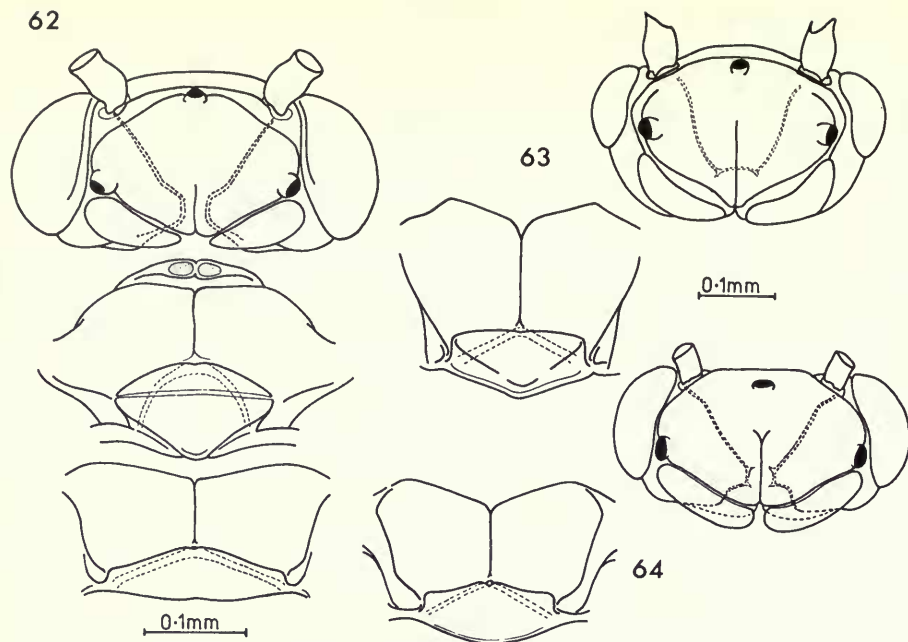
Afritrichia Mosely, 1939b : 35. Type-species: *Afritrichia aurea* Mosely, by original designation and monotypy. [Synonymized by Schmid, 1959a.]

Aratrichia Mosely, 1948 : 76. Type-species: *Aratrichia fahjia* Mosely, by original designation and monotypy. [Synonymized by Schmid, 1959a.]

Lamonganotrichia Ulmer, 1951 : 68. Type-species: *Lamonganotrichia crassa* Ulmer, by original designation and monotypy. **Syn. n.**

DISTRIBUTION. Palaearctic, SE. Asia, Africa.

McLachlan erected this genus for *fuscicornis* and a new species, *eatoniella*, the true identities of which were subject to a careful investigation by Kimmmins (1949). Larvae of the type-species were collected by Zeller from Messina (Sicily) along with the adults on which Schneider based his original description. Eaton (1873) referred to the biology of the larvae remarking that they '... at first roam at large, caseless; when they become corpulent they construct oval cylindrical cases of fine mud. They abound on rocks suffused with an extremely thin film of water resulting from the spray and dribbling of trickling streamlets, especially in places exposed to the sun!'; he was thus



Figs 62–64 Adult head and thorax, Stactobiini. 62, *Catoxyethira* sp.; 63, *Stactobia* sp.; 64, *Madioxyethira* sp.

the first to record both larval hypermetamorphosis in the Hydroptilidae and the madicolous habits of *Stactobia*.

Prior to Schmid's (1959a) paper on *Stactobia* the major contributions, albeit fragmentary, to the knowledge of the genus were by Mosely (1933), Vaillant (1951a; 1951b; 1952; 1956) and Botosaneanu (1956). Schmid subdivided the genus, which contains approximately 45 species, into four main species-groups, of which a summary of the main features is given below (partly adapted from Jacquemart, 1973). In the checklist the species are arranged according to these groups with new species (i.e. post Schmid, 1959a) being assigned correspondingly. Examination of the type of *Lamonganotrichia crassa* reveals that the genus *Lamonganotrichia* is synonymous with *Stactobia* according to structural affinities of the adult head, thorax and genitalia and similarities in the larva as described by Ulmer (1957).

DIAGNOSIS. Adult. Forewing length 1.5–4.0 mm: compound eyes relatively small; postoccipital lobes wide, suboval (Fig. 63); mesoscutellum narrow, deep (Fig. 63); spur formula 1.2.4 (Fig. 4) (0.2.4 in *radavanovici* Schmid); fore-coxae notched and fringed (Fig. 4); ♂ genitalia (Fig. 66) specialized; sternite VIII displaced posteriorly; segment IX reduced ventrally, often produced anteriorly as a pair of lateral apodemes; inferior appendages small, rarely elongate; subgenital appendages strongly sclerotized, arched; tergite X semimembranous; aedeagus long, straight, often considerably developed but sometimes thin and simple, usually with a dilated, heavily spined, membranous apex; ventral process of VII long, sinuous and thickened apically.

Larva. Early instars free-living, caseless, dorso-ventrally flattened and with tergites present on all abdominal segments. Fifth instars (Fig. 74) case-bearing, dorso-ventrally flattened; sclerotization well developed; setae modified as short, stout, protective spines. Sclerites of head fused; labrum symmetrical; mandibles (Fig. 30) not markedly asymmetrical, massive, heavily ridged, 'shovel-like', brushes present in both left and right (Botosaneanu, 1956); anterior ventral sclerites paired (Fig. 25); thoracic nota paired, medial lines distinct; preepisternite free on all three segments; sternites as in Fig. 38; legs short, subequal, robust, adapted for clinging; tergites present on all abdominal dorsa; posterior margin of tergite IX with 'crenellations' (modified flattened setae ?).

Case (Fig. 75). Dorso-ventrally compressed; transportable but usually temporarily fixed to substrate; barrel-shaped with dorsal and ventral longitudinal seams and slit-like anterior and posterior openings;

constructed of silk and fine grains of mud or sand. The case of *Lamonganotrichia* (Fig. 76, after Ulmer, 1957) is suboval or shield-shaped, with a central rectangular section occupied by the larva, and is bordered by a wide lateral folded fringe; a ventral longitudinal seam appears to be present.

BIOLOGY. The greatest contribution to the knowledge of the biology of *Stactobia* was made by Vaillant (1956) while detailed life-history data are given by Danecker (1961). The larvae are unique within the Hydroptilidae because they are madicolous (hygropetric, hydropetric), that is they are adapted to live in the tenuous habitat formed, according to Hynes (1970), by 'thin sheets of water flowing over rock faces' which 'although it is hardly a running-water habitat in the ordinary sense, it is often situated very close to one'. Thus the habitat often occurs at the edge of streams by the side of waterfalls and on rocky chutes, the faces of which may be almost vertical. Such conditions require very special structural adaptations of the inhabitants which can be clearly seen in the larvae and cases of *Stactobia* (Figs 74, 75). Both are dorso-ventrally flattened and capable of maintaining a thin film of water over their dorsal surfaces by surface tension; the cases are temporarily fixed but may be moved if conditions become unfavourable; the larvae are protected dorsally by heavily sclerotized fused tergites and spine-like setae and their short, robust legs are used for clinging to the substrate. The larval mouthparts are adapted for feeding on organic particles ('phytosaprophagous' according to Vaillant, 1956), the mandibles (Fig. 30) being robust, strongly ridged and having a scraping function. According to Vaillant (1956) the larvae are exclusively petrimadicolous, that is they occur only on rocky substrates almost devoid of sediment and filamentous algae. The pupae are often gregarious forming a 'Puppeneste' (Danecker, 1961) in which the cases are closely packed in a single 'colony'.

SPECIES-GROUPS (after Schmid, 1959a and Jacquemart, 1973). The *furcata*-group (20 species): this is the largest and most homogeneous group, its main feature being the constancy of the form of the male subgenital appendages; its distribution extends throughout central and southern Europe, the Atlantic Islands, North Africa, Israel and Turkey.

The *martynovi*-group (13 species); this is less homogeneous than the previous group and is characterized by the dorsal thickenings of tergite X and the anterior displacement of the inferior appendages of the males (most marked in *ulmeriana* Schmid to which, in my opinion, *schmidii* Kimmins from Nepal is most closely related); the group is restricted to southern Asia – Iran, Pakistan, Sri Lanka, Burma, Nepal and Turkestan (U.S.S.R.).

The *nielseni*-group (seven species including *Lamonganotrichia crassa*): this group is distinguished by the modified sternite VIII and the absence of any subgenital appendages in the males; representatives occur in Southern Yemen (Aden), Iran, Pakistan and Indonesia (Java).

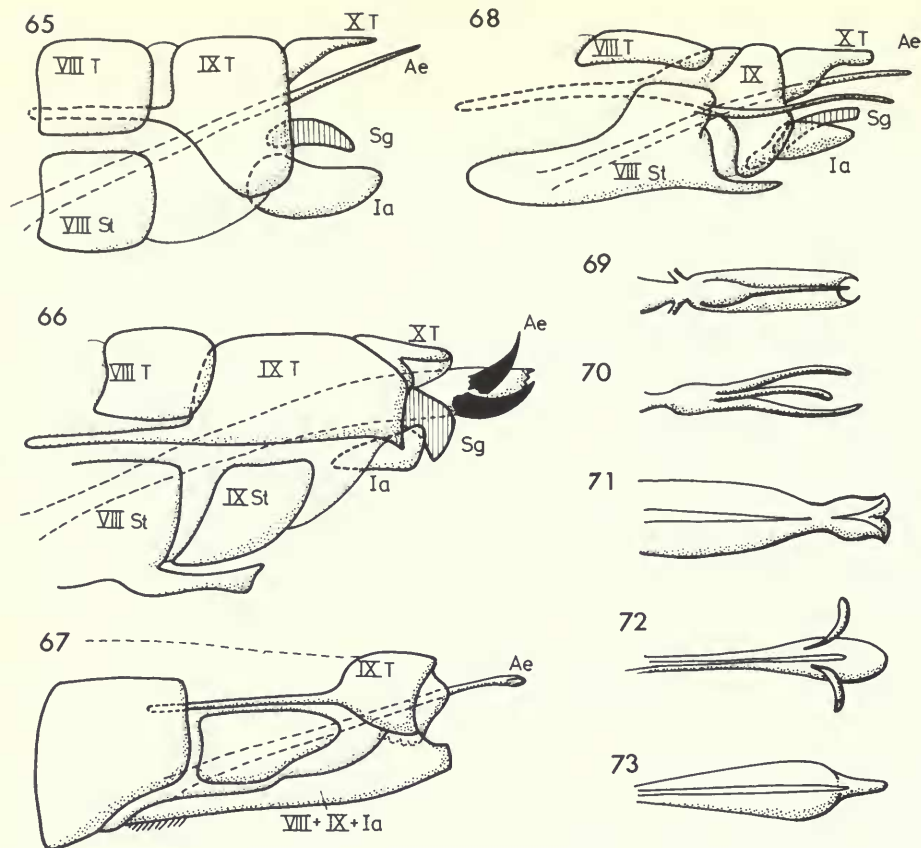
The *vaillanti*-group (two species): exclusively an African group with *vaillanti* Schmid from Guinea and *aurea* (Mosely) from Uganda.

S. bolzei Jacquemart (Turkey) is considered by Jacquemart (1965) to be distinct although I believe that it may belong to the *nielseni*-group (original description inadequate for direct comparison).

S. japonica Iwata (Japan) is known only from the larva of which the case bears more resemblance to that of *Plethrus* as figured by Ulmer (1957); the *japonica* of Tsuda & Nakagawa (1959) may be a distinct species since again only the larvae were examined.

S. megalatlantica Vaillant and *mallorcensis* Vaillant are nomina nuda.

DISCUSSION. *Stactobia* is a very specialized member of the Stactobiini. Although it is one of the more successful hydroptilid genera in terms of both species and individual numbers it does not have the widespread geographical ranges of, for example, *Hydroptila*, *Oxyethira* or *Orthotrichia*. The madicolous habits of the larvae perhaps enable *Stactobia* to occupy a niche where it is free from competition from these other genera, at least in the Palaearctic and parts of the Palaetropical regions. The absence of *Stactobia* from the New World may be due to two factors: (i) the slow rate of dispersal of montane stream-dwelling forms in comparison with lowland vegetation dwellers where geographic barriers are less pronounced (see later discussions) and (ii) competition with the highly successful New World Leucotrichiini which exhibit parallel modifications suiting them to a similar mode of life.



Figs 65–73 Generalized ♂ genitalia, Stactobiini. 65–68, lateral view, (65) *Stactobiella*, *Plethus*, *Chrysotrichia*; (66) *Stactobia* (after Schmid, 1959a); (67) *Madioxyethira*; (68) *Catoxyethira*. 69–73, aedeagus, dorso-ventral views, (69) *Stactobiella*; (70) *Chrysotrichia*; (71) *Madioxyethira*; (72) *Pseudoxyethira*; (73) *Catoxyethira*. (vide Figs 15, 16.)

Stactobia could have arisen from temperate or subtropical Palaearctic stock which penetrated southwards into Africa and SE. Asia and northwards into central Europe. It is totally absent from the northern Palaearctic region, there being no Scandinavian or British representatives of the genus.

Genus *PLETHUS* Hagen

Plethus Hagen, 1887 : 643. Type-species: *Hydroptila cursitans* Hagen, by monotypy.

Plethotrichia Ulmer, 1951 : 65. Type species: *Plethotrichia baliana* Ulmer, by original designation and monotypy. *Syn. n.*

DISTRIBUTION. S. and SE. Asia.

Plethus was erected for the type-species from Sri Lanka and now contains another five species from this island (Schmid, 1958a), one from Pakistan (Schmid, 1960) and three from Indonesia (Ulmer, 1951); the larvae of *acutus* and *cruciatus* were described by Ulmer (1957). *Plethotrichia baliana* was originally considered to be closely allied to *Plethus* but was separated on account of the unmodified larval case (Ulmer, 1957); a close examination of the adult features, however, indicates that the two genera are synonymous. *Stactobia japonica* Iwata from Japan also resembles *Plethus* in the form of the larval case.

DIAGNOSIS. *Adult*. Forewing length 1–2 mm: head and thorax similar to those of *Stactobia* (cf. Fig. 63): spur formula 0.2.3; wing venation greatly reduced; veins of forewing confluent before margin; veins of

hindwing reduced to the two main longitudinal subparallel stems of *R* and *M*; costal fringes well developed: ♂ genitalia (Fig. 65) simple, generalized without ventral processes; VIII unmodified; IX reduced ventrally although the sternite may be vestigial in some species, anterior apodemes short; inferior appendages unmodified; subgenital appendages heavily sclerotized, arched; tergite X variable; aedeagus long and straight without apical spines, sometimes with a pair of short basal processes: the anterior abdominal segments of the male may bear sensorial organs (Schmid, 1958a) which, in *baliana*, occur on tergites V and VI according to Ulmer (1951).

Larva (Fig. 77). Dorso-ventrally compressed; small abdominal tergites present, posterior margin of tergite IX simple; legs short, robust, subequal, unmodified; thoracic sternites as in Fig. 43.

Case (Fig. 78). Dorso-ventrally compressed, barrel-shaped with dorsal and ventral seams and a lateral fringe ('wings').

According to Ulmer (1957) the larvae of *Plethotrichia* are more like those of *Oeceotrichia* (here synonymized with *Hydroptila*) in that they are not dorso-ventrally compressed, there are no abdominal tergites and the fore-tibia bears a short process. The case is of the purse-type, flattened laterally and constructed of secretion and diatoms. However, the larvae were not reared and no pupae were collected to confirm the association of larvae and adults.

BIOLOGY. The larvae inhabit brooks amongst 'spongy algal masses' of *Cladophora* and 'siliceous' algae (Ulmer, 1957). According to Schmid (1958a) the adults are abundant by streams, fast-flowing rivers and rocky streams and are not attracted to light. The larvae are not hygropetric although Schmid (1958a) suspects that they live amongst the rocks in shallow water. According to Ulmer (1957) the larvae of *Plethotrichia* live in flowing water, springs (including warm springs), waterfalls and brooks, often in moss and algae.

DISCUSSION. The adults of *Plethus* retain many primitive features of the generalized stactobiine hydroptilid, their main specializations being their reduced size and wing venation and the presence of specialized male abdominal sensorial organs. The larvae, although adapted to live in fast-flowing shallow water, are not as specialized as the petrimadicolous larvae of *Stactobia*. *Plethus* is essentially a warm-adapted genus confined to the Oriental region.

Plethus is most closely related to *Stactobia* and was probably an early offshoot of the *Stactobia*-group branch of the Stactobiini and which has retained certain primitive attributes. Its main diagnostic features are the adult spur formula, overall reduced size and less specialized genitalia, larva and case (i.e. with respect to *Stactobia*).

Genus *STACTOBIELLA* Martynov

Stactobiella Martynov, 1924 : 57. Type-species: *Stactobia ulmeri* Siltala, by monotypy.

Tascobia Ross, 1944 : 124. Type-species: *Stactobia palmata* Ross, by original designation. [Synonymized by Ross, 1948.]

DISTRIBUTION. Holarctic.

Stactobiella is a small Holarctic genus containing six species, three of which are Palaearctic (northern and eastern Europe, Siberia) and three Nearctic which, according to Wiggins (1977), have been recorded over much of the North American continent west to the Rocky Mountain states and north to Minnesota, Ontario and Maine. *S. risi* from Switzerland was first described in *Microptila* but was transferred to *Stactobiella* by Ulmer (1929); Döhler (1963) synonymized *risi* with *ulmeri* but the species were later considered to be distinct by Botosaneanu (1967) and are regarded as such here. Ross (1944) gives diagnostic characters for the males and females of *delira* and *palmata* and (Ross, 1948) a key to the males of all six species.

The species are grouped below according to features of the male genitalia (after Ross, 1948).

The *biramosa*-group: *biramosa* (Siberia, 'Russia'); *palmata* (Oklahoma, Wisconsin, Illinois, Kentucky, Maine, Tennessee, Oregon).

The *ulmeri*-group: *ulmeri* (Finland, Germany, Poland, Rumania, U.S.S.R.); *risi* (Switzerland); *delira* (Wyoming, Colorado, Minnesota, Wisconsin, Maine, Kentucky, New Hampshire).

The *brustia*-group: *brustia* (Wyoming).

DIAGNOSIS. *Adult.* Forewing length 1.5–3.0 mm: metascutellum narrow, as wide as metascutum (cf. Fig. 62); spur formula 1.3.4: ♂ genitalia (Fig. 65) with segment VIII unmodified; IX well developed, especially dorsally, with long anterior apodemes; inferior appendages fused in *brustia*, sometimes with basodorsal bracteoles; subgenital plate strongly sclerotized, arched; tergite X absent or membranous; aedeagus (Fig. 69) simple, tubular, with fused lateral processes and a free median process in *delira*.

Larva (after Ross, 1944 and Wiggins, 1977). Body slightly compressed laterally: abdomen without tergites (except on segment IX); dorsal abdominal 'rings' present (II–VIII); legs short, subequal, stout; tarsal claws distinct, sharply curved and with thickened basal spur nearly half as long as claw (Fig. 80); setae unmodified: preepisternite free on all thoracic segments, episternite and epimeron fused in meso- and metathorax.

Case (Fig. 79). Purse-type, laterally compressed, constructed of silk only.

BIOLOGY. The larvae of *palmata* are found in small, fairly swift streams on stones in riffles and they mature in the early spring in Illinois (Ross, 1948). According to Wiggins (1977) it is therefore likely that this species overwinters as final instar larvae.

DISCUSSION. Adult features indicate that *Stactobiella* is related to *Stactobia* and *Plethus* although the metascutellum shows a close resemblance to those of *Chrysotrichia*, *Parastactobia* and *Catoxyethira*. The larvae are unspecialized and exhibit the basic hydroptilid form, the case being of the purse-type and laterally compressed. The genus thus appears to be an early offshoot of the Stactobiini which has retained many primitive larval and adult features. It is a temperate group which may have originated in the Palaearctic region and has had at least two subsequent migrations into the Nearctic region (via the Bering route) as indicated by the relationships of *delira* with *ulmeri* and *risi*, and of *palmata* with *biramosa*. The affinities with the other genera of the *Stactobiella*-group will be discussed later.

Genus *BREDINIA* Flint

Bredinia Flint, 1968c : 50. Type-species: *Bredinia dominicensis* Flint, by original designation and monotypy.

DISTRIBUTION. Lesser Antilles (Dominica).

The following diagnosis is adapted from the original description, the genus being known only from the type-series collected on Dominica in 1965. The larval stages are unknown.

DIAGNOSIS. *Adult.* Forewing length 1.5 mm: ocelli 3: mesoscutellum with transverse suture; metascutellum as wide as scutum, short and rectangular: spur formula 0.2.4: ♂ genitalia with sternite VIII divided mid-ventrally; IX narrow, oblique, lateral halves divided ventrally by the inferior appendages and with long anterior apodemes; tergite X a large membranous lobe; inferior appendages small, quadrate; subgenital plate elongate, rectangular; aedeagus tubular, apex flat and tridentate, central tubule in apical quarter.

BIOLOGY. The adults were taken only near the larger lowland rivers of the island.

DISCUSSION. Flint was uncertain of the relationships of this genus and simply listed its affinities with *Neotrichia* (presence of ocelli, minute size and spur formula), with *Mayatrichia* (spur formula) and with *Alisotrichia* (transverse suture of the mesoscutellum and lateral apodemes of segment IX in the male genitalia). Although Flint noted the similarity of the thoracic nota of *Bredinia* to those of *Stactobiella*, he did not consider these genera to be closely related. According to Flint's (1968c; 1970) descriptions, *Bredinia* bears more resemblance to *Stactobiella* than to *Alisotrichia*, especially with respect to the thoracic nota (cf. Figs 62, 83), the lateral apodemes of the male segment IX and the tridentate aedeagus (Figs 65, 69–73, cf. Fig. 84). The main distinction between *Bredinia* and *Stactobiella* is their spur formulae (0.2.4 and 1.2.4 respectively). As Flint notes, however, the affinities of *Bredinia* may be clarified when the larval stages have been discovered.

Genus *CHRYSOTRICHIA* Schmid

Chrysotrichia Schmid, 1958a : 54. Type-species: *Chrysotrichia hatnagola* Schmid, by original designation.

DISTRIBUTION. S. and SE. Asia (Sri Lanka, India and Sarawak).

Five species described from Sri Lanka (Schmid, 1958a) and India (Schmid, 1960) comprise this small SE. Asian genus. The immature stages are unknown but the adults appear to be closely

allied to those of *Stactobiella* according to features of the head, thorax and male genitalia. *Chrysotrichia* may be distinguished by its distinctive spur formula and reduced size and wing venation. Examination of more material, especially of the larval stages, will be needed before any definite conclusions regarding relationships can be reached. The following generic diagnosis is based on original descriptions and examination of paratype material in the BMNH collections.

Series of what may prove to be one or more new species of *Chrysotrichia* have recently been collected from Sarawak, 1977 (B. Bolton); 1978 (J. E. Marshall). The specimens are in the BMNH.

DIAGNOSIS. *Adult.* Forewing length 1.25–1.50 mm: head and thorax as in *Stactobiella* (Fig. 62): ocelli 3 (N.B. absent according to Schmid, 1958a): wings essentially reduced to thin 'ribbon-like' strips; venation represented by only two main longitudinal veins in the hindwings, veins of forewings reduced but not concurrent at the margin as in *Plethus*; costal fringes very long: spur formula 0.2.4: ♂ genitalia generalized as in *Stactobiella* and *Plethus* (Fig. 65); segment VIII simple; IX reduced ventrally, anterior apodemes present; inferior appendages small; subgenital plate strongly sclerotized, arched; tergite X membranous; aedeagus (Fig. 70) long, simple, with a trilobate apex and sometimes with minute apical spines (as in *hatnagola*).

BIOLOGY. According to Schmid (1958a) the adults occur along calm rivers at moderate altitudes. *C. badhami* from the Punjab was taken by a fairly large river rich in aquatic vegetation (Schmid, 1960).

DISCUSSION. Schmid (1958a) states that the male genitalia greatly resemble those of *Plethus* from which they may be distinguished by the small size and weak sclerotization of the two terminal segments in comparison with the remaining abdominal segments. The male genitalia are also similar to those of the *ulmeri*-group of *Stactobiella*; the diagnostic features at present used to distinguish this genus from *Chrysotrichia* (spur formula, wing size and venation) may not be as critical as originally thought and the genera may prove to be synonymous.

Genus *CATOXYETHIRA* Ulmer

Catoxyethira Ulmer, 1912b : 82. Type-species: *Catoxyethira fasciata* Ulmer, by monotypy.

Sperotrichia Marlier, 1978 : 294. Type-species: *Sperotrichia mali* Marlier, by original designation and monotypy. **Syn. n.**

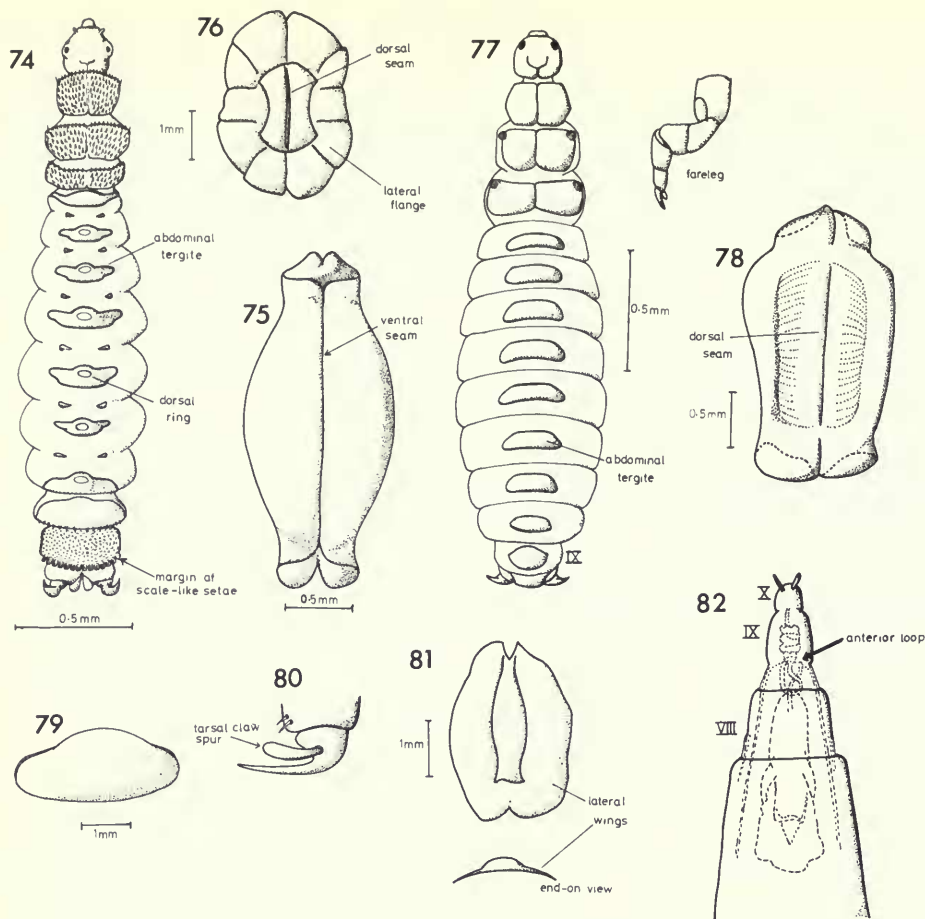
DISTRIBUTION. Africa.

Catoxyethira was erected for *fasciata* from Zaire by Ulmer (1912b) who described and figured the male genitalia. Ulmer (1912b) also outlined the main features of the larva and case of an unidentified species which he placed in *Catoxyethira* of which the generic identity is questionable since no positively determined adults were associated with it. *C. pinheyi* and *veruta* have since been described from the Victoria Falls and Rhodesia respectively and two new species, *ocellata* and *improcera* have been described by Statzner (1977) from Zaire; undetermined material collected by Prof. J. Medler from Nigeria is in the BMNH collection. Examination of the holotype and paratype of *Sperotrichia mali* from Mali reveals that this genus is synonymous with *Catoxyethira*.

As independently noted by Morse (1974), *Catoxyethira* has a number of structural affinities with the Holarctic genus *Stactobiella* especially with regard to the adult spur formula, thoracic nota and male genitalia. Although the latter are very specialized in *Catoxyethira* they may be derived from the basic stactobiine form. As Morse points out, however, further studies are needed to clarify the taxonomic limits of the genera.

Hydroptila formosae Iwata from Taiwan (Formosa) was described from the larva and case only, according to which Nielsen (1948) and Ulmer (1957 : 186) suggested that the species might belong in *Catoxyethira*. However, neither Nielsen nor Ulmer formally transferred the species which was done without reasoning by Fischer (1971) in his catalogue. Thus the species remains in *Catoxyethira* until examination of additional material can establish its true identity.

The generic diagnosis is based on examination of the following material (all in BMNH collections except where otherwise stated): *fasciata* (UHZIM); *pinheyi* (♂ type); *improcera* and *ocellata* (paratypes); undetermined species (Medler).



Figs 74–82 Stactobiini. 74–81, larvae and cases. 74–75, *Stactobia* (adapted from Vaillant, 1951b), (74) larva, dorsal view; (75) case, ventral view. 76, *Lamonganotrichia*, case, dorsal view (after Ulmer, 1957). 77–78, *Plethus cruciatus* Ulmer (after Ulmer, 1957), (77) larva, dorsal view, and foreleg, lateral view; (78) case, dorsal view. 79–80, *Stactobiella*, (79) case, lateral view; (80) larval tarsus, lateral view. 81, *Catoxyethira*, case, dorsal and end-on views (after Ulmer, 1912b). 82, *Madi-oxethira*, ♀ genitalia, ventral view.

DIAGNOSIS. *Adult.* Forewing length 1.5 mm: head and thorax as in *Stactobiella* (Fig. 62): ocelli 3 (cf. absent according to Ulmer, 1912b): spur formula 1.3.4 (cf. 0.3.4 according to Ulmer, 1912b): ♂ genitalia (Fig. 68) very specialized (main diagnostic feature of genus); sternite VIII elongate with a pair of posterior dorso-lateral spines; IX reduced, withdrawn into VIII, sternite may be present although small and fused with tergite, anterior apodemes narrow and produced beyond VIII; inferior appendages may be present (fused with tergite X in *veruta*); tergite X semimembranous in *veruta*, membranous and covered in microscopic setae in *pinheyi*; aedeagus long, straight, tapering to acute apex (Fig. 73) (the characteristic features of the male genitalia of *fasciata*, *pinheyi* and *veruta* are summarized by Morse, 1974).

Larva. Young larva 1.2 mm long, fifth instar 2.5 mm. According to Ulmer (1912b) the larva is somewhat similar in appearance to that of *Stactobia* from which it may be distinguished by the absence of the posterior 'crenellations' of tergite IX (cf. Fig. 74), the short spines of the posterior margin of tergite VIII and stout spines on tergites VIII and IX. According to Iwata (1928) *formosae* has sternites on abdominal segments III–V which do not occur in the African species of *Catoxyethira* and appear to be unique to this species within the Hydroptilidae.

Case (Fig. 81). According to Ulmer (1912b) this resembles the 'shield-case' of *Molanna* Curtis (Molanidae: Trichoptera) as it is dorso-ventrally flattened and has a central tubular region from which arise

the lateral 'wings'. The case, constructed of silk and fine sand-grains, tapers anteriorly and posteriorly and is attached to the substrate by the edges of the 'wings'.

BIOLOGY. Nothing is known of the biology of *Catoxyethira* but, from the dorso-ventrally flattened larva and fixed case, it would seem likely that the larva lives in fast-flowing water habitats such as swift streams (somewhat stony?). Ulmer's (1912*b*) specimens were taken from a tributary of the Butagu, Ruwenzori West (Zaire) at 1800 m, February 1908; the adults of *improcera* and *ocellata* (Statzner, 1977) were from a 'spring-brook' community (Kalengo stream, Zaire) and the larvae of *formosae* were taken in 'rapid mountain streams' (Iwata, 1928).

DISCUSSION. The form of the adult head and thorax indicate that *Catoxyethira* belongs to the *Stactobiella*-group of the Stactobiini. Discounting the dubious Taiwan species *formosae*, *Catoxyethira* appears to contain five exclusively African species which are characterized by the highly specialized and distinctive male genitalia. The uniqueness of the latter within the *Stactobiella*-group suggests that the ancestors of *Catoxyethira* reached Africa quite early in the history of the group and there evolved as a more tropical, warm-adapted line in isolation from the basic temperate stock. The recent discovery of a number of new species, all collected in considerable numbers, indicates that the genus is more widespread and successful than may have previously been thought.

Genus *PARASTACTOBIA* Schmid

Parastactobia Schmid, 1958*a* : 48. Type-species: *Parastactobia talakalahena* Schmid, by original designation and monotypy.

DISTRIBUTION. S. Asia (Sri Lanka).

Parastactobia is known only from the type-species in which the male genitalia are unique and difficult to homologize with those of any other hydroptilid. Examination of the female paratype (loaned by the USNM) has revealed that, contrary to Schmid's original description, three ocelli are present and that the thorax most closely resembles that of the *Stactobiella*-group (assuming that the female had correctly been associated with the male type). The immature stages are unknown.

DIAGNOSIS. *Adult.* Forewing length 1.75–2.25 mm: head and thorax as in *Stactobiella* (cf. Fig. 62); ocelli 3: spur formula 0.3.4: ♂ genitalia distinct (after Schmid, 1958*a*); segment IX with a large ventral notch (in which sternite VIII is completely encased) and a long asymmetrical dorsal spine and two tapering ventral appendages; tergite X reduced; aedeagus large with paired internal supports and a very complex apex.

BIOLOGY. Schmid (1958*a*) records the adults from beside a small, stony, fairly calm river in a dense forest in a small montane locality.

DISCUSSION. Little can be said regarding the relationships of *Parastactobia* until more adult (and larval) material is available for study. If the female paratype examined had been correctly associated with the male type then the genus would appear to be a highly specialized member (with respect to the male genitalia) of the *Stactobiella*-group as suggested by the structure of the head and thorax. I do not agree with Schmid (1958*a*) that the male genitalia resemble those of *Macrostactobia* (q.v.).

Genus *MADIOXYETHIRA* Schmid

Madioxyethira Schmid, 1960 : 89. Type-species: *Madioxyethira milinda* Schmid, by original designation and monotypy.

DISTRIBUTION. S. and SE. Asia (Pakistan, Nepal, Sarawak); Africa (Zaire, Congo).

Schmid erected this genus for the type-species from Pakistan. Kimmins (1964) described *nepalensis* from Nepal and Statzner (1977) has described a new species from Zaire (*marshalli*) which, on the basis of affinities of the metascutellum and the male and female genitalia, he has placed in *Madioxyethira*. The occurrence of the genus in the African continent is supported by the opinion that *Hydroptila trifurcata* Jacquemart from the Congo should rightly belong in *Madioxyethira*

according to the form of the male genitalia (however, the figures given by Jacquemart (1962a) are not easy to compare with those of established species). The immature stages are unknown.

A ♂ of what is possibly a new species of *Madioxyethira* was recently collected in Sarawak, 1978 (J. E. Marshall), in BMNH.

The following diagnosis is based on examination of the male type of *nepalensis* and a female paratype of *marshalli* (BMNH coll.).

DIAGNOSIS. *Adult.* Forewing length 2.25–3.25 mm: head and prothorax typical of the Stactobiini although the metascutellum (Fig. 64) is intermediate between those of *Stactobia* and *Stactobiella* (Figs 62, 63) and the postoccipital lobes are characteristically narrow: ocelli 3: spur formula 1.2.4, fore-tibial spur reduced to a small subspherical process (diagnostic): ♀ genitalia a typical oviscapit but with a characteristic loop in the anterior duct of the internal system (Fig. 82): ♂ genitalia very complex and difficult to homologize (Fig. 67); segment IX relatively small but produced anteriorly as a long point into the preceding segments; inferior appendages large, concave and ventrally prolonged as a unique plate which terminates on sternite VII; segment X forming two lateral obtuse plates ('bourrelet bombé' of Schmid, 1960) which Kimmins (1964) considers to be prolongations of tergite IX (Kimmins also considers that the 'inferior appendages' may have arisen from the fusion of sternites VIII and IX and the true inferior appendages); the aedeagus is narrow and simple in *milinda* while in *nepalensis* it has a complex apex divided into two narrow foliate lobes with two narrow divergent spines (Fig. 71).

BIOLOGY. According to Schmid (1960) *milinda* is common and abundant in parts of Pakistan between 1450 and 3000 m and its habits are exclusively madicolous (although Schmid did not collect or, therefore, examine larvae).

DISCUSSION. As will be shown later, *Madioxyethira* may prove to be synonymous with *Pseudoxyethira* Schmid and *Scelotrichia* Ulmer (in which case the last name takes priority). Schmid (1960) remarked on the possible synonymy of *Madioxyethira* and *Pseudoxyethira* since he could only distinguish these genera (apart from using genitalic features) on the venation of the hindwings, especially with respect to vein *ScR*.

Genus *PSEUDOXYETHIRA* Schmid

Pseudoxyethira Schmid, 1958a : 44. Type-species: *Pseudoxyethira asgiriskanda* Schmid, by original designation and monotypy.

DISTRIBUTION. S. Asia (Sri Lanka).

Only the adult stages of this highly specialized genus, represented by a single species from Sri Lanka, are known. Examination of a paratype female (USNM) reveals that the mesoscutellum and postoccipital lobes are identical to those of *Madioxyethira* (q.v.) (the specimen was returned before the significance of the fore-tibial spur and genital-duct loop were discovered and these were therefore not investigated).

DIAGNOSIS. *Adult.* Forewing length 2.75–3.00 mm: head and thorax as in *Madioxyethira* (Fig. 64): ocelli 3: spur formula 0.2.4 (according to Schmid, 1958a): ♂ genitalia very specialized with the ventral half of segment IX extending anteriorly as a plate to the middle of sternite VII, but not invaginated into the preceding segments; dorsal half of segment IX massive; appendages absent; aedeagus 'long and spiniferous' (Fig. 72).

BIOLOGY. According to Schmid (1958a) the adults frequent rivers at moderate altitudes and also elevated regions; they run about on rocks on the river banks.

DISCUSSION. If, as Schmid (1960) suggests, this genus is synonymous with *Madioxyethira* (q.v.) the name *Pseudoxyethira* takes priority. However, this is complicated by the possibility that *Scelotrichia* (see below) may also be a synonym since this would then take precedence.

Genus *SCELOTRICHIA* Ulmer

Scelotrichia Ulmer, 1951 : 73. Type-species: *Scelotrichia saranganica* Ulmer, by original designation and monotypy.

DISTRIBUTION. Indonesia (Java).

Only two male specimens of the type-species of this genus are known. The type-specimen of *saranganica* (UHZIM) was examined but was not in a condition favourable for the recognition of

critical features; however, the postoccipital lobes resemble those of *Madioxyethira* and the meso-scutellum has a transverse suture. The following diagnosis is partly adapted from Ulmer (1951).

DIAGNOSIS. *Adult.* Forewing length 2.8 mm: head as in *Madioxyethira* (Fig. 64); thorax with transverse mesoscutellar suture (cf. Fig. 62); ocelli 3: spur formula 1.2.4, fore-tibial spur minute (Ulmer, 1951: pl. 2, figs 31B, C): ♂ genitalia difficult to interpret from Ulmer's figures.

DISCUSSION. According to features of the head and mesothorax, *Scelotrichia* is a member of the Stactobiini. The shape of the postoccipital lobes and the presence of a small fore-tibial spur (and also the general appearance of the male genitalia) indicate that the genus may be very close to, if not synonymous with, *Madioxyethira* and *Pseudoxyethira* (see above); in that case the senior name would be *Scelotrichia*. Further examinations of material and discovery of the larval stages are required to establish the true identities of these genera.

Tribe **LEUCOTRICHINI** Flint **stat. n.**

Leucotrichinae Flint, 1970: 2. Type-genus: *Leucotrichia* Mosely, 1934.

DISTRIBUTION. North, Central and South America.

Flint (1970) erected the subfamily Leucotrichiinae (as Leucotrichinae) for the distinct group of Nearctic and Neotropical hydroptilids consisting of *Leucotrichia* and its closely related genera. Since the group has many of the features characteristic of the Hydroptilinae in general it is considered here at the status of tribe.

The tribe is predominantly of Central American distribution (including the West Indies) although a few species occur in North America while some are found as far south as Chile in South America; the latter continent is very under-collected and will undoubtedly yield many new species.

Flint (1970) stated that he could give no single character by which the group could be distinguished from other hydroptilids in the adult stages but he did list the following as being diagnostic when present: ocelli reduced to 2; head modified; antennae modified; reflexed costal cell (basal costal 'pouch' or 'bulla') present on male forewing. Flint did not define the basic structure of the male genitalia although, in his words, 'there is . . . something characteristic' about their form. As will be shown in the diagnosis given below, the adults of the Leucotrichiini do possess a number of distinguishing features which clearly set the group apart from the other hydroptiline tribes; the larvae (at least in those genera which are known) also appear to be very distinct due to their structural modifications associated with their torrenticolous habits. The following list of diagnostic adult and larval characters has been based on an examination of Mosely's type-material (BMNH) and a study of Flint's (1970; 1972b; 1974) papers on *Leucotrichia* and related genera.

The tribe Leucotrichiini is considered to contain those genera originally included by Flint (1970), with the addition of *Celaenotrichia*, of which Flint considered *Alisotrichia* to be distinct according to features of the male aedeagus, the female genitalia and the larval stages. The tribe thus contains the *Leucotrichia*-group: *Leucotrichia*, *Zumatrichia*, *Peltopsyche*, *Anchitrichia*, *Costatrichia*, *Acostatrichia*, *Betrichia*, *Abtrichia* and *Celaenotrichia*, and the *Alisotrichia*-group: *Alisotrichia*.

DIAGNOSIS. *Adult.* Forewing length 1.2–4.0 mm; wings brilliantly coloured, sometimes spangled with green and silver; the male forewing sometimes has a basal costal pouch (bulla) which may contain modified setae; head and tentorium well developed, former often with modifications in the male; antennae generally short, of approximately 13–20 segments, male basal or median segments sometimes modified; ocelli 3, often reduced to 2 in the male (rarely also in the female); mesoscutellum with transverse suture; metascutellum pentagonal or subtriangular: spur formula 1.3.4 (except *Alisotrichia*, 0.2/3.3/4); fifth abdominal segment with typical lateral setose processes: ♀ genitalia a simple oviscapt, internal apparatus well developed (in *Alisotrichia* segment VII is modified and the internal apparatus is simple and 'ring-like'); ♂ genitalia (Fig. 84) often with ventral processes; sternite VIII distinct, produced posteriorly beneath segment IX, sometimes with postero-lateral processes; segment IX fused, incomplete ventrally, sometimes with postero-lateral processes; inferior appendages narrow, short, rod-like, basically unmodified but sometimes fused medially and bearing baso-dorsal bracteoles; tergite X membranous or well sclerotized, fused latero-ventrally with the subgenital appendages which may be indistinct or developed as heavily

sclerotized plates; latter fused ventrally with subgenital plate which may be produced ventrally and may articulate with an unidentified structure lying between the inferior appendages; aedeagus (Fig. 84) an elongate tube with a median constriction and (except in *Alisotrichia*) a complex medial structure consisting of a basal loop and a pair of basally directed processes, sometimes with a pair of circular 'windows' in lateral view, apex membranous with various spinose processes and lateral plates.

Larva (Figs 85–89, 92). Larvae have been associated with *Leucotrichia*, *Zumatrichia*, *Peltopsycha*, *Anchitrichia*, *Abtrichia* and *Alisotrichia*; they typically exhibit hypermetamorphosis (Flint, 1970), the early instars being entirely free-living and caseless. From a specimen of what would appear to be a young larva from a small collection of *Peltopsycha sieboldii* Müller (BMNH collection), the early stages are dorso-ventrally flattened with slender, tapering abdomens and short, robust clinging legs; there is a single tergite on each abdominal segment and the long, slender anal prolegs project laterally from the sides of segment X. In all genera (except *Alisotrichia*) the final (fifth) instar builds a permanently fixed case in which it remains throughout the stage. The fifth instar exhibits structural modifications suiting it for such a sedentary existence in comparison with the earlier free-living stages: the body again is dorso-ventrally flattened; the ecdysial lines of the rugose or papillate head are variously fused, as are those of the meso- and metathoracic nota; the legs are short and robust; the abdomen is distended, especially segments V and VI which are abruptly enlarged, and small tergites are present on segments I–VIII while tergite IX is large, shield-shaped and sometimes bears enlarged spine-like setae; the anal prolegs are fused to the sides of segment X, the claws alone being free. The genus *Alisotrichia* is unique in that the fifth instar larva does not construct a case until just prior to pupation. The larva accordingly retains the structural adaptations of the earlier stages (cf. Figs 92, 51) with a slender, tapering abdomen, large abdominal tergites (i.e. relative to the size of the segments) and long, slender, freely projecting anal prolegs which are not fused to the sides of segment X.

Case (Fig. 86). The cases of the Leucotrichiini are said to resemble leech egg-cases. They are strongly depressed dorso-ventrally and composed of tough secretion, rarely embedded with small inorganic particles, and sometimes with transverse strengthening ridges; the dorsal surface is slightly vaulted while the flat ventral surface is firmly attached to the substrate; there is a small circular opening at either end.

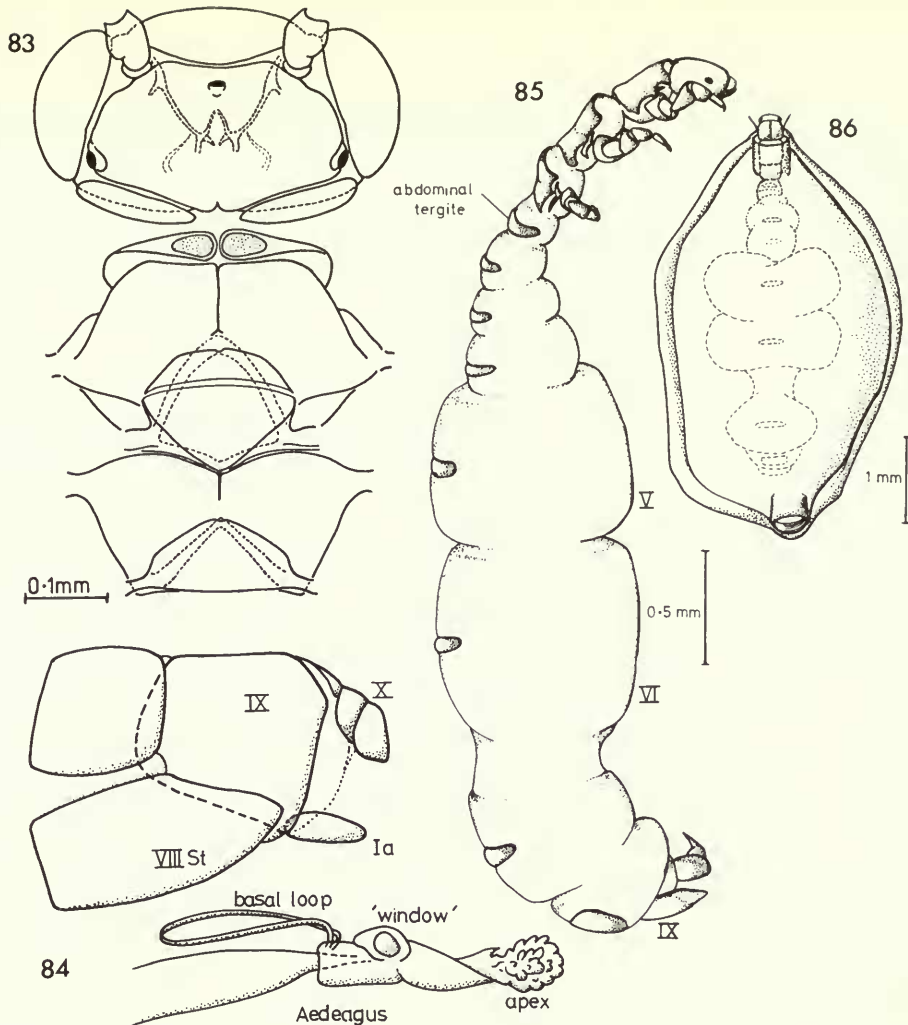
Pupa. Typically hydroptilid: mandibles long, without teeth. The pupal case varies between genera and species but basically resembles the larval case with sealed anterior and posterior ends. In *Alisotrichia hirudopsis*, where the case is not built until just before pupation, the central suboval region is surrounded by an irregular flange by which the case is attached to the substrate and which has two to six small round openings (possibly for water circulation according to Flint, 1964; 1970). In *A. spangleri* the pupal case is torpedo-shaped and is attached to the substrate from one end by a silk thread 2–8 mm long (Flint, 1970); in this way the case floats freely just below the surface of the water and this may serve to prevent desiccation due to fluctuating water levels (Flint, 1970).

BIOLOGY. The larvae (early and fifth instars) are adapted to live in torrenticolous conditions, usually being found in great numbers on boulders in the rapid sections of fast-flowing rivers. Some are also found in the thin surface film of water on partly exposed rock surfaces moistened by spray from nearby cascades (similar to the madicolous habitat of *Stactobia*). Structural modifications include dorso-ventral flattening, fixed cases, well-developed and fused sclerites, protective spinose setae and short robust clinging legs.

The larvae are reported to feed on 'periphyton' and small particles of detritus on the surrounding rock surfaces. In the case-dwelling forms the larva extends its slender anterior end through either of the narrow case openings and grazes on the immediate surroundings. The larva never leaves the case and this, in the later stages of the instar, would be impossible anyway due to the distension of the middle abdominal larval segments. The retention of the free-living habit by the final instar of *Alisotrichia* may be an adaptation serving to increase the feeding range of the larva. In all genera the mandibles are adapted for scraping and grazing as they are strong with blade-like, sometimes dentate, edges.

The adaptation of the pupal case of *Alisotrichia spangleri* for the prevention of desiccation due to fluctuating water levels shows a remarkable parallelism with that of the larva of *Rhyacopsyche hagenii* which also inhabits a torpedo-shaped case anchored by a thread to the substrate; however, in this species, the pupal case is fixed.

Adult Leucotrichiini are reported to be most active on the exposed parts of the rocks on which the larvae dwell. They prefer bright sunlight and congregate on the rock surfaces and run around often describing semicircular paths. Such habits are typical of hydroptilids in general.



Figs 83-86 *Leucotrichia*. 83, adult head and thorax, dorsal view; 84, generalized ♂ genitalia, lateral view (vide Figs 15, 16); 85, larva, lateral view; 86, larva in case, dorsal view.

DISCUSSION. As can be seen from the generic key, couplets 13 to 19, it has not been possible to define the genera of the Leucotrichiini satisfactorily since species from two or more genera often key out with one another (e.g. *Abtrichia* and *Betrichia*; *Costatrachia* partim, *Betrichia* partim, *Leucotrichia* partim and *Celaenotrichia*). Flint (e.g. 1972b; 1974) appears to be very inconsistent in his choice of criteria when assigning new Neotropical species to genera, using features of the head, antennae and wings in some cases and genitalic features in others. Genera were originally erected on the basis of certain (then apparently distinctive) characters common to a group of species from a particular geographical area but, as new species have been discovered from other areas, the generic limits do not appear to be so clear-cut. The larval generic key is also very unsatisfactory at present since it is based on only a few species of each genus (only one in some cases and, in *Anchitrichia*, association with adults is purely assumptive). The tribe is thus in need of a thorough review which, however, would probably best be done by American workers due to the location of most of the material.

In general, however, the Leucotrichiini appears to form a distinct group within the Hydroptilinae and is characterized by a number of both adult and larval features. The origins of the tribe

are speculative but the ancestral form appears to have given rise to a very specialized group with an essentially Central American distribution. In this region the ecological conditions favour short generation cycles resulting in high speciation rates and species diversity.

The tribe has greatest superficial affinities with the essentially Old World Stactobiini, particularly the *Stactobia*-group. Common adult features are the short antennae, the transverse meso-scutellar suture (cf. Figs 62, 83) and the simple basic form of the male genitalia (cf. Figs 65, 84) while the larvae are similarly dorso-ventrally flattened, have clinging legs, protective abdominal tergites, modified setae and fixed cases (cf. Figs 74, 75, 77, 78, 85–87, 92). However, the larval similarities between the Leucotrichiini and the *Stactobia*-group are probably due to their comparable madicolous habits since they are all functional and protective adaptations to living in this type of aquatic habitat and are also seen in a number of unrelated insect groups (see Vaillant, 1956; Hynes, 1970). The larvae of the two tribes may be distinguished by certain fundamental differences in, for example, the form of the head, the complete fusion of all thoracic nota (i.e. medially) and the characteristic enlargement of the abdomen in the Leucotrichiini; the cases of the Leucotrichiini do not have dorsal and ventral seams and are of a different shape. The adults differ in the shape of the metascutellum, the reduced spur formula of the Stactobiini and the different modifications of the male genitalia.

Nevertheless, the Leucotrichiini and the Stactobiini appear to have more in common with one another than with any other group of hydroptilids and may have arisen from a common ancestor very early in the evolutionary history of the Hydroptilinae. This common ancestor may have arisen in the Old World temperate region and given rise to two main lines, one of which colonized the cool, montane streams of the Palaearctic and Palaetropical regions (the present-day Stactobiini) while the other penetrated the American continent (probably via the Bering connection) and passed down to the Central American region where the descendants of these early arrivals evolved into the highly successful Neotropical Leucotrichiini.

However, this hypothesis is tentative and further evidence from new species and distribution records is required in order to present a more accurate picture of the evolutionary history of the Leucotrichiini. The tribe may prove to be more distantly related to the Stactobiini than indicated above, the morphological similarities being the result of convergent rather than parallel evolution. In conclusion the Leucotrichiini is a very specialized and successful member of the Hydroptilinae which has a predominantly Central American distribution and may share a common ancestry with the Stactobiini.

Genus *LEUCOTRICHIA* Mosely

Leucotrichia Mosely, 1934 : 157. Type-species: *Leucotrichia melleopicta* Mosely, by original designation.

DISTRIBUTION. North and Central America and the Antilles.

Leucotrichia contains ten species of predominantly Central American distribution although *sarita* and *limpia* have been recorded from the southern United States, while *pictipes* is widespread throughout the U.S.A. (but not so far recorded from Canada). The larva of *pictipes* was first described by Lloyd (1915) (as *Ithytrichia confusa*) and larvae have now been associated with all species except *melleopicta*, *virida* and *fairchildi*.

DIAGNOSIS. *Adult*. Forewing length 2–5 mm: dorsal region of head sometimes modified; ocelli 3 or 2 (♂ only): metascutellum pentagonal (Fig. 83): wings unmodified: spur formula 1.3.4: ♂ genitalia simple (Fig. 84) with a single posterior spine or paired setal brushes on sternite VII; sternite VIII posteriorly produced beneath segment IX; IX completely open ventrally, postero-lateral margin with a row of stout setae; tergite X heavily sclerotized; subgenital plate connected dorsally to tergite X and produced ventrally as a narrow, elongate mesal sclerite which projects down to the base of the inferior appendages; subgenital appendages small, semimembranous; inferior appendages unmodified, elongate and usually fused meso-ventrally; aedeagus with median complex and spinous, membranous sac-like apex (Fig. 84).

Larva (Fig. 85). Typical of the Leucotrichiini but with the following characteristics: head rugose or papillate; pronota with antero-lateral angles not produced; femora with spiniform dorsal setae, tarsal claw single; abdominal tergites II–VII smaller than in *Zumatrachia*, without central pores; tergite IX rarely with enlarged basal setae (after Flint, 1970).

Case (Fig. 86). Typically flat, silken, ovoid and slightly domed.

BIOLOGY. According to Wiggins (1977) the larvae occur on rocks in strong currents of running water where they graze on the surrounding periphyton and detritus. Collection data indicate that *pictipes* probably overwinters as a final instar larva and pupates from May to August.

SPECIES-GROUPS. Flint (1970) splits the genus into two main species-groups on the basis of adult features.

The *melleopicta*-group is characterized by the three ocelli in both sexes, the unmodified male head (except in *chiriquiensis*) and the single process of sternite VII in the male.

The *pictipes*-group is distinguished by the males having only two ocelli, a modified head (except in *imitator*) and a brush of setae or a point on sternite VII.

Flint (1970) gives keys to the males of all species and to all described larvae.

Genus *ZUMATRICHIA* Mosely

Zumatruchia Mosely, 1937 : 187. Type-species: *Zumatruchia filosa* Mosely, by original designation.

DISTRIBUTION. North and Central America and the Antilles.

Zumatruchia contains 18 species of essentially Central American distribution although *notosa* is known from Montana only and was originally described in *Leucotrichia*. The immature stages are known only for *antilliensis*, *anomalopecta* and *multisetosa*.

DIAGNOSIS. *Adult.* Forewing length 2.5–4.0 mm: head unmodified; ocelli 2 (♂), 3 (♀); male basal antennal segment elongate, enlarged, with a 'button-like' appendage which covers half of the slightly concave face (cf. Fig. 91): mesoscutellum pentagonal; wings unmodified: spur formula 1.3.4: ♂ genitalia (cf. Fig. 84) with a short ventral process on sternite VII; sternite VIII produced beneath segment IX, sometimes with a pair of lateral processes; segment IX open ventrally with a postero-lateral lobe or process; tergite X is heavily sclerotized and sometimes produced posteriorly; subgenital appendages large and plate-like, fused with subgenital plate ventro-medially; inferior appendages usually fused baso-medially and often with a baso-dorsal bracteole; aedeagus with median complex and membranous apex bearing spines and plates.

Larva (Fig. 87). Typical of the *Leucotrichiini* but distinguished by the rugose, but non-papillate, head; simple pronota; femora with spiniform baso-dorsal setae (according to Wiggins, 1977, paired tarsal claws are present in *antilliensis*); abdominal tergites larger than those of *Leucotrichia* and with paired contiguous central pores; tergite IX covered in short, stout, spinous setae.

Case. Typically flat, silken (sometimes with embedded sand-grains), ovoid and dome-like (cf. Fig. 86).

BIOLOGY. Wiggins (1977) states that the larvae inhabit fast-flowing sections of running-water (preferring larger rivers according to Flint, 1968a). The larvae of *antilliensis* have successfully adapted to living on boulders in the fast-flowing sections of the larger lowland rivers of Dominica (Flint, 1968a).

SPECIES-GROUPS. Flint (1970) splits the genus into five species-groups (here reduced to four) on the basis of features of the male genitalia.

The *multisetosa*-group (lobe of segment IX multisetate).

The *galtena*-group (sternite VIII without lateral processes, bracteole present).

The *filosa*-group (sternite VIII with lateral processes, no bracteole).

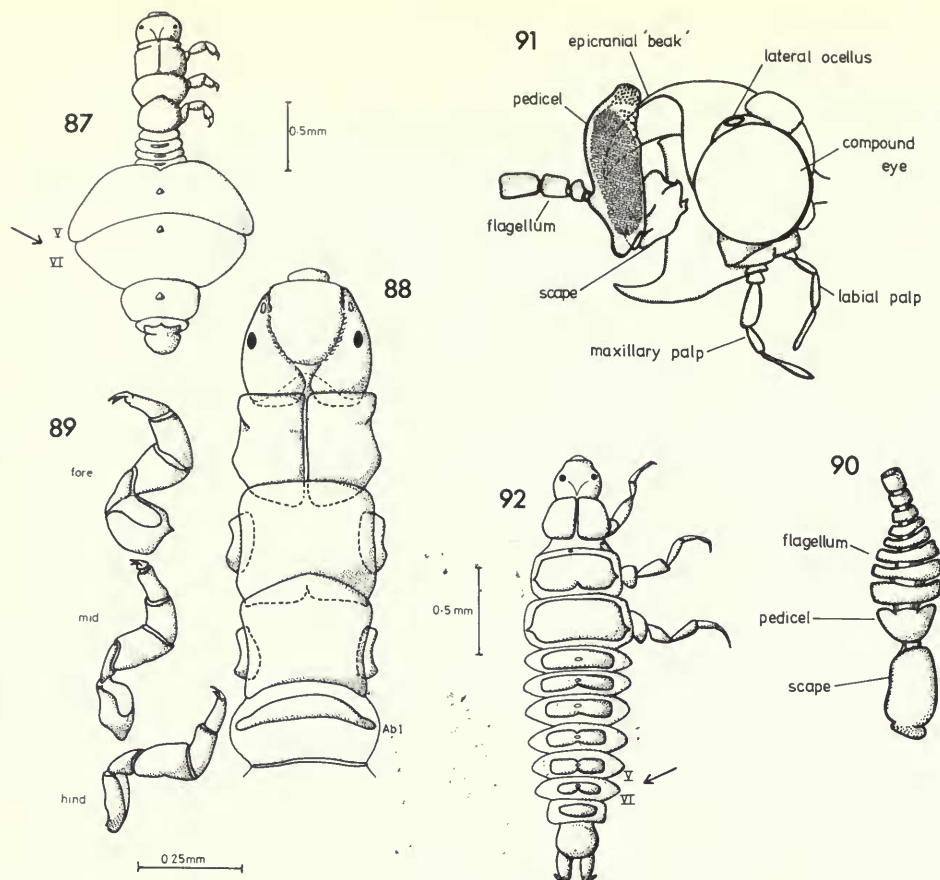
The *palmara*-group (sternite VIII with lateral and ventral processes, bracteole present; Flint, 1970, distinguishes *anomalopecta* and *palmara* on the colour and structure of the forewing only).

Genus *PELTOPSYCHE* Müller

Peltopsyche Müller, 1879c : 144. Type-species: *Peltopsyche sieboldii* Müller, by subsequent designation by Fischer, 1961.

DISTRIBUTION. Brazil.

This genus is known only from descriptions and crude figures of two species collected by Müller from the Santa Catarina region of southern Brazil. Although Müller (1879b; 1879c; 1880) gave a general account of the habitat and adults he only figured the general larval form and the basal antennal segments of the males of both species. Thus, since Müller's original adult specimens have not been traced, the genitalia and, therefore, the true identities of the two species remain unknown. However, I have been able to examine larvae and cases of *sieboldii* which were sent to McLachlan by Müller and are now in the BMNH collection.



Figs 87–92 Leucotrichiini. 87, *Zumatrichia antillensis* Flint, larva, dorsal view (after Flint, 1970). 88–89, *Peltopsyche sieboldii* Müller, larva; (88) head and thorax, dorsal view; (89) thoracic legs, lateral views. 90, *Costatrichia lodora* Mosely, ♂, basal antennal segments; 91, *Abtrichia squamosa* Mosely, ♂, head, lateral view (after Mosely, 1939c); 92, *Alisotrichia hirudopsis* Flint, larva (fifth instar), dorsal view (after Flint, 1970).

The actual spelling of the name of the type-species is in need of clarification. Müller continually used *sieboldii* except in a communication to McLachlan which was published in the Proceedings of the Royal Entomological Society (Müller, 1879b) where he used *sieboldi*. *P. sieboldi* was used by Ulmer (1907) and Fischer (1961) lists the species under this name with all of Müller's references to *sieboldii* being treated as synonyms even though Fischer was aware that *sieboldii* was the first published name. I therefore propose to accept Müller's original orthography.

The following diagnosis is based on Müller's original descriptions with additional observations on the larvae in the BMNH collection. The genus is clearly a member of the Leucotrichiini according to the general appearance of the larvae and the modified male antennae.

DIAGNOSIS. Adult. According to Müller the adults are distinguished by the modified basal segments of the male antennae (13-segmented, longer in the female). In *maclachlani* the second segment is merely somewhat longer and wider than the others, but in *sieboldii* this segment is enlarged, ovoid and bears a small, rounded process as in *Zumatrichia*. Müller suggests that these structures may have an 'odoriferous' function. The spur formula is quoted as 2.4.4 but this may be an error, the usual leucotrichiine count being 1.3.4.

Larva (Figs 88, 89). According to Müller's descriptions and figures the abdomen of the larva is greatly distended in segments V–VII and fills nearly the entire case (cf. Figs 85, 87) and is thus typical of the Leucotrichiini. Examination of the BMNH specimens of *sieboldii* (dried and originally glued to card)

reveals that the general morphology is very similar to that of *Zumatrichia* with respect to the head, legs, thoracic nota, wide abdominal tergites (with their paired contiguous central pores) and the short, stout spines of segment IX; unlike *Z. antilliensis*, however, the tarsal claws are unpaired, according to Wiggins (1977).

Case. This is identical to that of *Leucotrichia*, being ovoid and flattened ('leech egg-case' case); the dorsal surface is transversely ridged in *sieboldii* and smooth in *maclachlani*.

Pupa. According to Müller this is remarkable for the unusually great difference in the 'complicated cornus patches dorsally on the abdomen' between the two species. He is probably referring to the pre- and postsegmental dorsal abdominal plates but, since Müller does not describe the specific differences, I cannot comment on their significance.

BIOLOGY. The cases were found in very large numbers fixed to the upper side of stones in rapids in the larger tributaries of the Itahajy (Garcia, Encana, Warnow, etc.), Santa Catarina. *P. maclachlani* was only found in a single rapid near the mouth of the Warnow along with *sieboldii*.

DISCUSSION. *Peltopsyche* may prove to be a senior synonym of one or more genera of the Leucotrichiini described subsequently by Mosely and Flint (see later discussion).

Since Müller obviously encountered what he identified as *sieboldii* in a number of localities more than one species may be involved; this problem will only be resolved when Müller's original material has been located and examined.

Genus *ANCHITRICHIA* Flint

Anchitrichia Flint, 1970 : 14. Type-species: *Anchitrichia spangleri* Flint, by original designation and monotypy.

DISTRIBUTION. Central America (Mexico, Guatemala, Honduras, Costa Rica, Panama).

This genus contains only the type-species and is very closely related to *Zumatrichia* from which it is distinguished by a number of adult features including its relatively larger size (4–5 mm forewing length), its habit of holding its wings roof-like over the body, the unmodified antennae, the presence of 2 ocelli in both sexes, and the general form of the male genitalia (cf. Fig. 84). The larva, described by Flint (1970), was not reared but associated 'by supposition' and is distinguished by the bilobed anterior margin and postero-medial process of the frontoclypeus, the enlarged antero-lateral angles of the pronota, the arborescent baso-dorsal seta of the femur and the form of the abdominal tergites. The larval case is typical of the Leucotrichiini but has an enlarged, transversely oval, protective hood at one end and a flared collar at the other. The pupal case is unique in that it is quite unlike that of the larva, being torpedo-shaped and attached at one end to the substrate by a silk strand 2–8 mm long. In this way the case floats just below the surface of the water and may be an adaptation to prevent desiccation due to fluctuating water levels and appears to parallel the condition seen in the larval case of *Rhyacopsyche* (Fig. 99).

The true status of *Anchitrichia* has yet to be established; the examination of more species is required to define the limits of the genus. It may prove to be synonymous with one or more of the other leucotrichiine genera.

Genus *COSTATRICHIA* Mosely

Costatrichia Mosely, 1937 : 166. Type-species: *Costatrichia lodora* Mosely, by original designation and monotypy.

DISTRIBUTION. Central America.

Costatrichia was erected for a single Mexican species and now contains three additional species from Panama (Flint, 1967a; 1970), one from Nicaragua and one from El Salvador (Flint, 1970). The immature stages are unknown.

DIAGNOSIS. *Adult.* Forewing length 2.0–2.5 mm; head unmodified; ocelli 3; basal antennal segments simple, middle segments sometimes broad and flat (Fig. 90); metascutellum subtriangular; forewing often with basal costal 'bullae' (Fig. 10); spur formula 1.3.4: ♂ genitalia (cf. Fig. 84) with lateral processes often on sternite VIII; segment IX with setose postero-lateral processes; tergite X strongly sclerotized and fused with segment IX; subgenital appendages elongate, separate, often with baso-dorsal bracteoles; aedeagus with median complex and spinose membranous apex.

SPECIES-GROUPS. Flint (1970) splits the genus into two distinct species-groups on the basis of features of the male genitalia, head and wings.

The *simplex*-group (*simplex*, *spinifera*): unmodified antennae, no basal costal bulla.

The *lodora*-group (*lodora*, *panamensis*, *tripartita*, *bipartita*): modified antennae, basal costal bulla present.

Flint (1970) gives a key to separate the males of all six species. He distinguishes the genus from *Zumatrachia* by the presence of three ocelli and the unmodified basal segments, but sometimes modified middle segments, of the male antennae.

Genus *ACOSTATRICHIA* Mosely

Acostatrachia Mosely, 1939c : 228. Type-species: *Acostatrachia plaumanni* Mosely, by original designation.

DISTRIBUTION. South America (Brazil, Surinam).

Mosely erected this genus for two south Brazilian species, *plaumanni* and *simulans*, and Flint (1974) later described three new species from Surinam. The immature stages are unknown.

DIAGNOSIS. *Adult*. Forewing length 2.0–2.5 mm: head unmodified; ocelli 3; antennae unmodified; forewing with basal costal pouch (cf. Fig. 9) filled with broadened hairs: spur formula 1.3.4: ♂ genitalia (cf. Fig. 84) usually with two short ventral processes on segment VII; sternite VIII with postero-lateral processes; inferior appendages sometimes with bracteoles; aedeagus with median complex and spinose membranous apex.

DISCUSSION. The three Surinamese species are said by Flint (1974) to resemble the two original Mosely species although the basic form of the male genitalia is slightly different (but not enough to warrant the erection of a new genus). According to Flint, *fimbriata* is closest to *brevipenis*, while *spinifera* resembles *simulans* and *plaumanni*. As Mosely (1939c) points out, the genus is closely related to *Costatrachia* Mosely, differing only in features of wing venation and in having unmodified antennae but, again as noted by Mosely, these may be specific rather than generic characteristics (see later discussion). The larvae will probably prove to be of the general *Leucotrachia* type, as will those of *Costatrachia*.

Genus *BETRICHIA* Mosely

Betrachia Mosely, 1939c : 230. Type-species: *Betrachia zilbra* Mosely, by original designation and monotypy.

DISTRIBUTION. South America (Brazil, Argentina).

Erected for a single Brazilian species, this genus now also contains *argentinica* from north Argentina and *surinamensis*, *bispinosa* and *occidentalis* from Surinam (Flint, 1972b; 1974).

Mosely gives no precise reasons for erecting this genus but it may be assumed that it was mainly on account of venational and antennal features as well as the general form of the male genitalia; in the male type-specimen (BMNH) there are 2 ocelli, the antennae are 19-jointed with an elongate basal segment. Flint (1972b) places *argentinica* in this genus on genitalic features alone although there are 3 ocelli and the antennae are simple. Of Flint's (1974) Surinamese species only *occidentalis* resembles the type-species, while in *surinamensis* the head is greatly modified and the genitalia are quite different; in *bispinosa*, although the genitalia resemble those of *zilbra*, the forewing has a basal costal pouch. Flint (1974) states that 'he would prefer to wait until the South American fauna is better known . . . before erecting more genera' but I am of the opinion that all the small leucotrachiine genera, such as *Betrachia*, *Costatrachia* and *Acostatrachia* for example, should be grouped together as the characters originally given as diagnostic generic features are now proving to be specific instead; this, however, will be discussed more fully later. As such no precise diagnosis of the genus *Betrachia* can be given; only the main features are listed below. The immature stages are unknown.

DIAGNOSIS. *Adult*. Forewing length 2–4 mm: head and antennae slightly modified or simple; ocelli 2 or 3: forewing with or without basal costal pouch: spur formula 1.3.4: ♂ genitalia (cf. Fig. 84) with a process on sternite VII; sternite VIII usually without postero-lateral processes: segment IX with or without postero-lateral processes; inferior appendages fused medially; tergite X and subgenital plate variable; aedeagus with median complex and spinose membranous apex.

DISCUSSION. As is evident from the above account this genus is very difficult to key out satisfactorily. As with a number of other genera in the Leucotrichiini all species descriptions must be referred to before a specimen suspected of belonging to *Betrichia* can be positively identified.

Genus *ABTRICHIA* Mosely

Abtrichia Mosely, 1939c : 224. Type-species: *Abtrichia antennata* Mosely, by original designation.

DISTRIBUTION. South America (Brazil, Argentina).

Abtrichia was erected for two very distinct species from southern Brazil, *antennata* and *squamosa*, of which the former has since been recorded, along with its immature stages, from northern Argentina by Flint (1972b). *Abtrichia* is characterized by the highly modified head of the male with the enlarged, process-bearing, basal antennal segment (Fig. 91) and the large basal costal pouches of the male forewings which contain small scales or coarse hairs (Fig. 9). According to Flint (1972b), the larvae bear most resemblance to those of *Zumatrichia antilliensis*, differing only in having a papillate dorsal head surface.

DIAGNOSIS. *Adult*. Forewing length 4 mm: head of male modified with dorsal and ventral anterior beak-like processes (Fig. 91); ocelli 2 (both sexes); antennae 12-jointed in the male with an enlarged, process-bearing, basal segment (Fig. 91): forewing with costal pouch along basal half (Fig. 9): spur formula 1.3.4: ♂ genitalia (cf. Fig. 84) with a short process on sternite VII; sternite VIII and segment IX without postero-lateral processes; subgenital appendages well developed; inferior appendages distinct, with or without bracteoles; aedeagus with median complex and spinose membranous apex.

Larva and case. Typical of the *Leucotrichia*-group.

BIOLOGY. According to Flint (1972b) the cases are tightly attached to rocks in riffles.

Genus *CELAENOTRICHIA* Mosely

Celaenotrichia Mosely, 1934 : 158. Type-species: *Celaenotrichia edwardsi* Mosely, by original designation and monotypy.

DISTRIBUTION. South America (Chile).

C. edwardsi was originally described from Chiloe Island and Flint and Barria have since collected additional specimens (USNM) of which I have examined a female example. From the adult features the genus appears to belong in the Leucotrichiini; it is characterized by the unmodified antennae and forewings and the distinctive genitalia of the male. The immature stages are unknown.

DIAGNOSIS. *Adult*. Forewing length 3 mm: head and antennae simple, latter 26-segmented; ocelli 3: forewings unmodified: mesoscutellum with transverse suture; metascutellum pentagonal: spur formula 1.3.4: ♂ genitalia relatively simple (cf. Fig. 84) with a process on sternite VII; sternite VIII produced postero-ventrally, without postero-lateral processes; segment IX open ventrally with deep postero-dorsal V-shaped cleft enclosing the membranous tergite X which has two narrow longitudinal supporting sclerites; subgenital appendages heavily sclerotized and spinose; subgenital plate well developed; inferior appendages curved inwards, without bracteoles; aedeagus appears to have a median complex (microscope slide preparation of the type-specimen (BMNH) indistinct here), apex membranous and spinose.

Genus *ALISOTRICHIA* Flint

Alisotrichia Flint, 1964 : 46. Type-species: *Alisotrichia hirudopsis* Flint, by original designation and monotypy.

DISTRIBUTION. Central America (including the Antilles).

Alisotrichia contains 12 species, three of which are also known in their larval stages, and is a member of the Leucotrichiini but forms a distinct subgroup according to both adult and larval features. The insects are very small and, although adult characters are somewhat variable, constant diagnostic features include the absence of a fore-tibial spur, the simplified aedeagus and modified tergite VII of the male and the simple internal apparatus of the female genitalia. The larvae are unique within the tribe in that the fifth instars remain free-living until pupation and thus retain the general appearance of the earlier instars of this and other leucotrichiine genera (cf. *Ugandatrichia*). The following diagnosis is adapted from Flint (1970).

DIAGNOSIS. *Adult.* Forewing length 1.2–2.5 mm: basal antennal segment of male often enlarged; ocelli 2 or 3: metascutellum pentagonal to subtriangular: spur formula 0.2.4, 0.2.3 or 0.3.4: ♀ genitalia simple, tergite VII modified (no details or figures given by Flint, 1970), internal apparatus with a simple ring or sphere: ♂ genitalia (cf. Fig. 84) with sternite VIII and segment IX often with postero-lateral processes; inferior appendages, tergite X, subgenital appendages and plate very variable and difficult to interpret; aedeagus simple with a median constriction and a simple to complex internal structure but never with a midlength complex (basal loop, 'windows', etc.).

Larva (Fig. 92). Abdomen not distended, tapering posteriorly; tergites I–VIII covering most of dorsum of each segment and each with three contiguous central pores, tergite IX shield-shaped without pores; anal prolegs long, projecting freely from segment X.

Pupal case (after Flint, 1964, for *hirudopsis*). This is built just prior to pupation and is similar to the typical leucotrichiine larval and pupal case. It is silken, dorso-ventrally flattened, with an ovoid central region (containing the pupa) which is surrounded by an irregular flange which attaches the case to the substrate and has two to six small round openings (for water circulation ? (Flint, 1964)).

BIOLOGY. The larvae of *hirudopsis* are found on rocks in fast-flowing water at various altitudes and occur abundantly on exposed boulders kept wet by the spray from nearby cascades. The adults are also abundant and run about in the sunlight on the dry exposed parts of the rocks on which the larvae live.

SPECIES-GROUPS. Flint (1970) splits the genus into several groups of species on the basis of adult characters such as the number of ocelli, spur formula and antennal modifications. However, as Flint does not define the groups clearly, I have not discussed them here.

DISCUSSION. The fifth instar larva of *Alisotrichia* conforms to the basic leucotrichiine plan but retains the free-living adaptations of the earlier instars; on the basis of this and the characteristic adult features this genus would appear to be a specialized and distinct member of the Leucotrichiini and is placed here in its own subgenus.

Tribe OCHROTRICHIINI trib. n.

Type-genus: *Ochrotrichia* Mosely, 1934.

DISTRIBUTION. North and Central America.

The tribe Ochrotrichiini is proposed here for the small group of Nearctic and Neotropical hydroptilids composed of *Ochrotrichia* (*O. Ochrotrichia* and *O. Metrichia*) and *Rhyacopsyche*. As will be discussed in more detail below, *Metrichia* was reduced to a subgenus of *Ochrotrichia* by Flint (1972a) on the larval affinities, Flint (1971) having previously indicated the relationships of the adults of *Metrichia* and *Rhyacopsyche*. The relationships of these genera have not been thoroughly investigated due to the lack of comparative material. Flint's views have therefore been accepted and, as the group exhibits a number of characteristic adult features which distinguish it from the other hydroptiline groups, it has been accorded the status of tribe. However, this arrangement is not entirely satisfactory and the group may subsequently prove to be a subgroup of the tribe Hydroptilini. This will be discussed in more detail in the discussion below.

DIAGNOSIS. *Adult.* Forewing length 1.5–3.5 mm: head and antennae unmodified (Fig. 93); tentorium complete; ocelli 3; postoccipital lobes small, subspherical: mesoscutellum with transverse suture (Fig. 93); metascutellum pentagonal or convexly subtriangular: spur formula 0.3.4 or 1.3.4: abdomen with typical hydroptiline setate processes of segment V: ♀ genitalia a simple oviscap: ♂ genitalia variable but basically with segment VIII unmodified and inferior appendages well developed and elongate.

Larva (Figs 97–99). General appearance typical of basic, unspecialized hydroptilid: head unmodified, labrum symmetrical: three pairs of thoracic nota, each divided by a distinct median line: abdomen distended, slightly compressed; abdominal tergites absent except on segment IX; anal prolegs fused to sides of segment X.

Case. Variable between genera: basic 'purse-type' hydroptilid case in *Ochrotrichia*, usually covered in fine sand grains; modified in *Rhyacopsyche* as an elongate, tubular case tapering at both ends and attached at one end to the substrate by a short silken thread.

Pupa. No description available, but probably of the typical hydroptiline form with long, untoothed mandibles.

DISCUSSION. The Ochrotrichiini is a distinct, warm-adapted, New World group of the subfamily Hydroptilinae. It may be distinguished from the Leucotrichiini, with which it shares the feature of a transverse mesoscutellar suture, by the characteristic and highly specialized male genitalia and the basic hydroptilid appearance of the larva. The tribe may later prove to be a subgroup of the Hydroptilini but is provisionally treated here as distinct on the basis of certain fundamental morphological and behavioural features. These include the presence of a transverse mesoscutellar suture and the characteristic male and female genitalia (including the absence of a spiral 'titillator' on the male aedeagus) and the associations of the larvae with running water habitats and their possible detritus-feeding habits (cf. the predominantly algal-feeding habits of the Hydroptilini). However, such features may be secondarily derived from the basic Hydroptilini condition, a thorough examination of representative adult and larval material being essential for the establishment of the true relationships of the group within the Hydroptilinae and of the genera with one another.

Genus *OCHROTRICHIA* Mosely

Ochrotrichia Mosely, 1934 : 162. Type-species: *Ochrotrichia insularis* Mosely, by original designation and monotypy.

DISTRIBUTION. North, Central and South America.

The genus *Ochrotrichia* has recently been reviewed by Denning & Blickle (1972) who list the 40 known species and give descriptions of 15 additional new species from the western United States and Mexico. In the same year Flint (1972a) published a paper on 'The genus *Ochrotrichia* from Mexico and Central America (Trichoptera : Hydroptilidae)' in which he described a number of new species and proposed *Metrichia* as a subgenus of *Ochrotrichia*, and *Rhyacopsyche* as a close, but distinct, relative. Flint (1968b) had already stated his views regarding the congenericity of *Metrichia* and *Ochrotrichia* but they were not accepted by Denning & Blickle (1972). As it has not been possible to investigate this question in detail due to the paucity of material in the BMNH collections, Flint's views have been accepted here. There is obviously a need for a thorough and critical review of the group to establish the relationships of the genera concerned and to investigate the position of the group within the Hydroptilinae.

DIAGNOSIS (*Ochrotrichia* sensu Flint, 1972a). *Adult*. Forewing length 1.5–3.0 mm: head unmodified; tentorium complete (Fig. 93); antennae simple (c. 33-segmented in *insularis*); mesoscutellum (Fig. 93) with transverse suture; metascutellum convexly subtriangular: spur formula 0.3.4 or 1.3.4: ♀ genitalia a simple oviscapit; internal surface of sternite VIII often sclerotized and reticulate in *Ochrotrichia* (*Metrichia* not described): ♂ genitalia distinct (Figs 94–96) with segment VIII unmodified; segment IX fused, annular, deeply incised dorsally; tergite X often highly developed with numerous spines and processes; inferior appendages usually strongly developed, basically broad and elongate, usually with various processes and rows of spines; aedeagus simple and thread-like (*Ochrotrichia*), sometimes armed with strong spines (*Metrichia*).

Larva (Fig. 97) after Flint (1972a). General appearance typically hydroptilid: head unmodified; mandibles robust, broadly subtriangular, medial brush in left only: meso- and metanota with pronounced antero-dorsal processes; prothorax with a pair of anal sternites (Fig. 44, after Wiggins, 1977); pleurites well developed (at least on prothorax): abdomen similar to that of *Hydroptila* (cf. Fig. 118) being slightly distended and laterally compressed; dorsal 'rings' present.

Case. Similar to that of *Hydroptila*; constructed of two laterally compressed silken valves, 'purse-type', covered in fine sand-grains and, occasionally, filamentous algae (Wiggins, 1977); sometimes the case consists of a single dorsal convex valve carried 'tortoise-shell' like, the ventral valve being flat and of secretion only.

Pupa. No description available.

BIOLOGY. The larvae occur in a wide variety of running water habitats (rivers to warm streams and cold springs) and temporary streams according to Ross (1944); the specimens with cases carried 'tortoise-shell' like were from a spring stream on rocks in a thin film of water; the feeding habits are unknown but it is possible that the larvae are detritus feeders.

Key to subgenera (adults) (adapted from Flint, 1972a)

- 1 Spur formula 0.3.4; ♂ inferior appendages and tergite X complex, aedeagus simple and thread-like **OCHROTRICHIA** (p. 186)
- Spur formula 1.3.4; ♂ inferior appendages and tergite X simple, aedeagus with well-developed spines **METRICHIA** (p. 186)

Subgenus **OCHROTRICHIA** Mosely

Polytrichia Sibley, 1926 : 102. Type-species: *Ithytrichia confusa* Morton, by monotypy. [Preoccupied by *Polytrichia* Borg de St Vincent, 1831 in Protozoa.]

Ochrotrichia Mosely, 1934 : 162. Type-species: *Ochrotrichia insularis* Mosely, by original designation and monotypy. [Synonymized with *Polytrichia* by Mosely, 1937 and reinstated by Ross, 1944.]

This subgenus is distributed throughout the U.S.A., with a few species recorded from southern Canada, Panama and the Antilles, although the group appears to be predominant in the midwest and montane regions of the United States.

DIAGNOSIS. *Adult.* Spur formula 0.3.4; ♂ genitalia with inferior appendages and tergite X often very complex, aedeagus simple and thread-like.

The subgenus contains about 70 species which Flint (1972a) splits into two distinct groups (for the Central American species only). The *xena*-group is characterized by the male genitalia with its relatively simple segment IX and tergite X and the aedeagus, which varies from a simple tube to one which bears various processes (not as well developed as in *Metrichia*). It appears to be the simpler of the two groups with respect to the structure of the male genitalia and also seems to be intermediate between the next group and *Metrichia*. The group contains *xena*, *unio*, *flagellata*, *pectinata*, *brayi*, *caligula*, *marica*, *spinosissima* and *verda*.

The second group consists of all other Central American and Antillean species which Flint (1972a) further splits into six subgroups; the group is characterized by the fusion of tergites IX and X in the male genitalia to form a complex structure bearing many spines and plates (Fig. 95, terminology after Ross, 1941b), and also the very simple, thread-like aedeagus. A key to the males of the Central American species is given by Flint (1972a).

Larvae have been associated with the following species: *anisca*, *riesi*, *spinosa*, *tarsalis*, *unio* and *xena*, a key to which is given by Ross (1944). According to Flint (1972a), the larvae of this subgenus are found in running water, usually in small to moderately sized streams, sometimes in very shallow water and often in streams that dry up during the dry season. Flint also remarks that the adults come readily to light unlike those of *Metrichia*.

Subgenus **METRICHIA** Ross

Metrichia Ross, 1938 : 9. Type-species: *Orthotrichia nigrutta* Banks, by monotypy.

Argentitrichia Jacquemart, 1963 : 339. Type-species: *Argentitrichia bulbosa* Jacquemart, by monotypy.

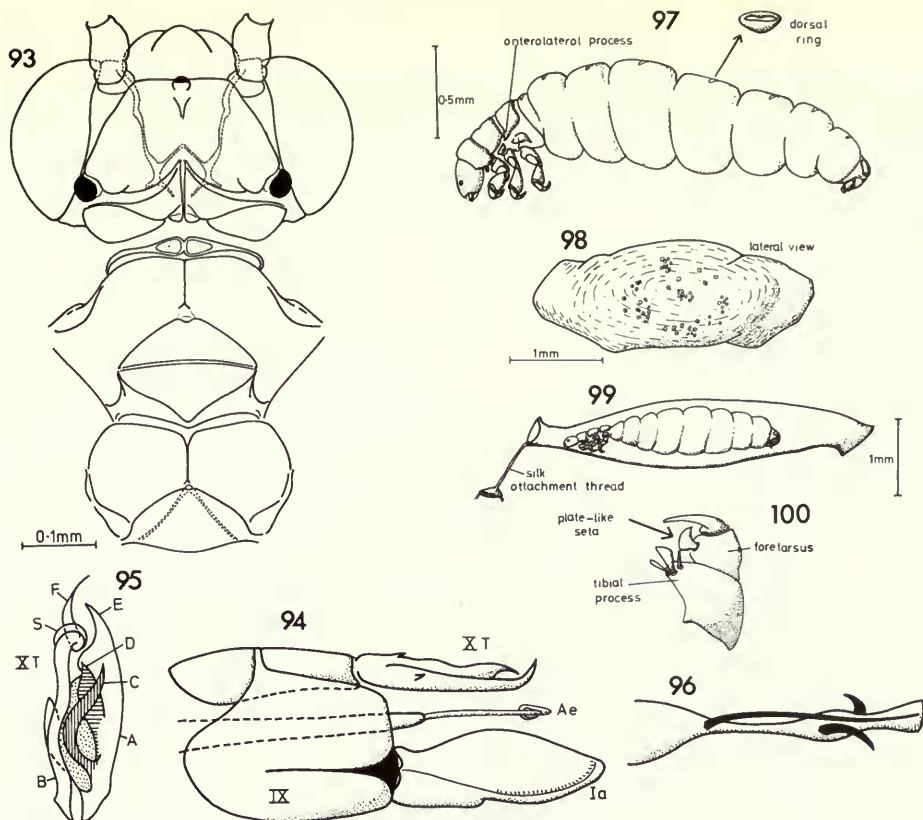
Syn. n.

This subgenus has a more southerly distribution than *Ochrotrichia*, occurring in the south-west United States, throughout Central America and the Antilles, Peru, north-west Argentina, central Chile and Surinam. According to Flint (1972a) the area of greatest diversity occurs throughout Central America and the Antilles.

DIAGNOSIS. *Adult.* Spur formula 1.3.4; ♂ inferior appendages and tergite X simple, aedeagus with well-developed spines; ♂ with internal abdominal sacs (between IV–V, V–VI or VI–VIII) and dorso-lateral hair brushes on abdominal segments V and VI.

There are 19 distinct species of which Flint (1972a) splits the Central American representatives into five groups on the basis of the presence and positioning of the internal abdominal sacs of the males, the dorso-lateral hair brushes and the structure of the aedeagus (Fig. 96). Flint also gives a key to the males of the Central American species.

Larvae have been associated with *nigrutta* by Edwards & Arnold (1961) and *juana* by Flint (1968a). According to Flint (1972a) the larvae build 'purse-type' cases of silk and organic particles. On the basis of features of the two known species, Flint concludes that the subgenus appears to



Figs 93–100 Ochrotrichiini. 93, adult head and thorax, dorsal view, *Ochrotrichia*. 94–95, *Ochrotrichia* (*Ochrotrichia*); (94) lateral view; (95) tenth tergite, dorsal view (terminology after Ross, 1941b). 96, *O. (Metrichia)*, aedeagus, lateral view (vide Figs 15, 16). 97–98, *Ochrotrichia* (*O.*) *jauna* Flint; (97) larva, lateral view; (98) case, lateral view. 99–100, *Rhyacopsyche mexicana* (Flint); (99) larva in case, lateral view; (100) larval foretibio-tarsus, lateral view.

be closely associated with springs, seeps, waterfalls and the like (rather than the larger, relatively more slowly flowing streams preferred by *Ochrotrichia*). Flint also states that the adults are more frequently taken by sweeping vegetation than at light.

Flint (1972a), following Schmid (1958a), considers *Metrichia* to be most closely related to the Palaearctic genus *Microptila* (sensu Schmid, vide the Hydroptilini, *Agraylea*-group) on the basis of the form of the male genitalia and wing venation. He also recognizes the possibility that *Microptila* may eventually come to be considered as a third subgenus of *Ochrotrichia*. As will be seen in the account of *Microptila*, *Metrichia* is really very dissimilar to and quite distantly related to *Microptila*. These conclusions were based on a comparative study of features of the head, thorax and male genitalia of the two groups.

Finally, *Argentitrichia bulbosa*, described by Jacquemart (1963) from the Argentine, appears to be a species of *Metrichia* according to the characteristic form of the male genitalia (material not examined).

Genus *RHYACOPSYCHE* Müller

Rhyacopsyche Müller, 1879a : 40. Type-species: *Rhyacopsyche hagenii* Müller, by subsequent monotypy. *Rhyacopsyche* Müller, 1879c : 143.

DISTRIBUTION. Central America.

Müller (1879a) erected *Rhyacopsyche* for a single Brazilian species, which he subsequently

(1879c) named *hagenii*, on the basis of the larval cases only. Figures and full descriptions of the larval and pupal cases were not published until 1880 by Müller, the first descriptions of the adults and larvae being given by Thienemann (1905). Möller (1921) subsequently reproduced a previously unpublished figure by Müller of the general appearance of the larva.

Following the discovery of immature and adult stages of *Metrichia mexicana* in Guatemala (first described from Mexico by Flint, 1967a), Flint (1971) considers this species to be congeneric with *Rhyacopsyche hagenii*. Consequently Flint (1971) described the genus *Rhyacopsyche* and gave a key to the males of *mexicana* and three new species.

DIAGNOSIS (after Flint, 1971). *Adult*. Forewing length 2.5–3.5 mm: head and antennae simple; ocelli 3: mesoscutellum with transverse suture (cf. Fig. 93); metascutellum pentagonal: spur formula 1.3.4: ♀ genitalia a simple oviscapt, tergite VIII with posterior lobes; ♂ genitalia with segment VIII unmodified; IX produced into dorso-lateral lobes; tergite X contracted inside lobes of IX; inferior appendages large and distinct, elongate and curved upwards; single, reduced, median subgenital sclerite; aedeagus with tubular basal half, apical half with central tube and thin spiral filament, apex with thickened spine.

Larva (Fig. 99). Typically hydroptilid with thoracic nota present on all three segments, divided medially; sternites apparently absent; legs short, subequal; apex of fore-tibia with a distinct process bearing several enlarged setae; tarsus short with one or two enlarged, plate-like setae (Fig. 100): abdomen distended, slightly compressed; tergites absent; anal prolegs fused to segment X.

Case (Fig. 99). Larval case elongate, tubular, tapering at both ends; silken, covered in sand grains (*mexicana*) or of secretion only (*hagenii*); attached to substrate by a long silken thread from the anterior end. Pupal case of *mexicana* apparently split along posterior end according to the figure in Flint (1971), but this may have been drawn after emergence of the pharate adult; pupal cases of both *mexicana* and *hagenii* anchored by a short silken stalk.

BIOLOGY. The larvae and pupae of *mexicana* were found on an exposed boulder subjected to constant wetting from spray and a thin film of water running down from a nearby cascade. The pupal cases were attached at right angles to the boulder on the moist, but not submerged, surfaces. According to Flint (1971) the larval cases of *mexicana*, unlike those of *hagenii*, are not attached by a thread to the substrate until just prior to pupation.

DISCUSSION. According to Flint (1971) the adults of *Rhyacopsyche* may be distinguished from those of *Metrichia* only by the form of the male and female genitalia (the lobes of segment IX and the relatively simple aedeagus of the male and the lobes of tergite VIII of the female in *Rhyacopsyche*). The larvae of *Rhyacopsyche* are, according to Flint (1971), very similar to those of *Ochrotrichia* s.l. and *Hydroptila*, being distinguished by the plate-like setae of the fore-tibia and the hook-like tarsal claws. The larval and pupal cases are, however, so far unique to *Rhyacopsyche* and are probably adapted to exposed conditions in fast-flowing water, being fusiform and anchored by a silk thread to the substrate.

The morphology of the larva has not been described in sufficient detail to allow a deeper investigation into the generic relationships of *Rhyacopsyche* but adult features suggest that the genus is closely allied to *Ochrotrichia* s.l. I do not agree with Schmid (1958a) and Flint (1971) that these genera are closely related to *Microptila* (q.v.).

Tribe NEOTRICHIIINI Ross

Neotrichiini Ross, 1956 : 18. Type-genus: *Neotrichia* Morton, 1905.

DISTRIBUTION. Nearctic, Neotropical.

Ross first used the name Neotrichiini in a phylogenetic diagram (Ross, 1956 : 18, chart II) showing the coincidence of the primitive lines of Trichoptera with the 'cool-adapted habitat', the Neotrichiini representing a specialized 'warm-adapted' offshoot of the main Hydroptilini branch. Ross, however, did not then or subsequently define the tribe although he is still of the opinion that the group should be maintained as distinct from the rest of the Hydroptilidae, principally on account of the characteristic form of the larvae and their 'Limnephilid-like' cases (Ross, *in litt.*). Therefore, although Ross's (1956) classificatory scheme has been modified here in that the Hydroptilini sensu Ross are treated as a subfamily, the status of the Neotrichiini is retained as originally proposed.

The Neotrichiini consists of two exclusively warm-adapted New World genera, *Neotrichia* and *Mayatrichia*, the combined distribution of which extends from Canada, through the United States and Central America (the regions of greatest species and individual numbers) down into central Argentina. The genera share a number of unique adult and larval characters which distinguish them from all other Hydroptilinae, although they still retain the basic diagnostic features of this subfamily. As indicated above, the immature stages characterize the Neotrichiini since the larvae construct cylindrical cases, with circular anterior and posterior openings, reminiscent of the higher limnephiloid groups and quite unlike the basic 'purse-type' case of the Hydroptilidae. The larvae accordingly exhibit parallel limnephiloid-like morphological features associated with the form of the case. These include the cylindrical abdomen and the free anal prolegs which may be extended through the wide posterior opening of the case, and in one species of *Neotrichia* a lateral line appears to be present.

The following diagnosis is based on Ross (1944) and examination of adult material in the BMNH collection and larvae of both genera (USNM loan).

DIAGNOSIS. *Adult.* Forewing length 1.5–2.0 mm: head and antennae simple; tentorium complete; ocelli 3: mesoscutellum without transverse suture, anterior margin convex; metascutellum convexly subtriangular: fore-tibia without apical spur: abdomen with typical lateral setate processes on sternite V: ♀ genitalia a simple oviscap: ♂ genitalia (Fig. 101) – segment VIII unmodified; IX fused, annular, open postero-ventrally, well-developed postero-lateral processes present; inferior appendages and subgenital plate well developed; bilobed process sometimes present and often may be fused to the underside of the subgenital plate in some species of *Neotrichia*; tergite X usually membranous with various lobes; subgenital appendages present (homologies uncertain).

Larva (Figs 102, 104–106). Head conical, tapering anteriorly, antennae relatively long (cf. other Hydroptilidae): thoracic nota paired: abdomen only slightly distended, cylindrical, abruptly enlarged from segment II, from there gradually tapering posteriorly; tergites VIII and IX present only, latter covering whole of dorsum; anal prolegs slender, long, projecting freely from segment X; lateral fringe of short setae ('lateral line') sometimes present along sides of abdomen: thoracic legs slender, tarsal claws long.

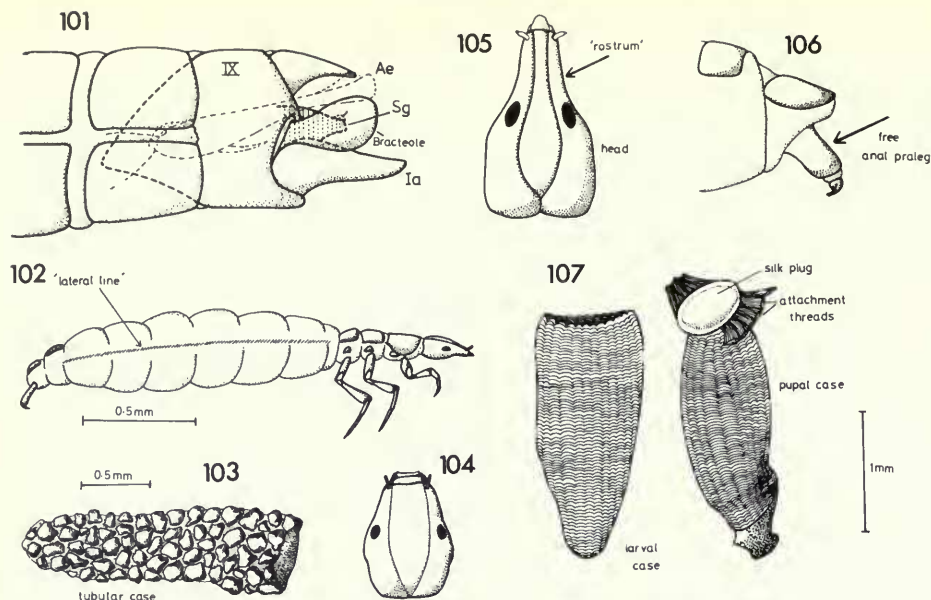
Case. Cylindrical, slightly tapering posteriorly, constructed of secretion only (surface strongly ridged) (Fig. 107) or with a covering of small sand-grains (Fig. 103); openings suboval to circular, wider anteriorly.

BIOLOGY. Larvae occur on rocks in rapid sections of rivers and streams; details of feeding habits unknown, but probably detritus-feeders; according to Wiggins (1977) the guts of three specimens of *Mayatrichia* contained almost exclusively fine organic particles although, from the shape of the head, he suspects them to have specialized feeding habits.

DISCUSSION. The Neotrichiini is exclusively a New World group containing two very closely related genera which are distinguished from each other by features of the male genitalia, adult spur formula and the general form of the larva. The structure of the adult thorax and presence of the spiral aedeagal process in the males of *Neotrichia* indicate that the group may have arisen relatively recently from the main Hydroptilini branch and evolved its characteristic features in isolation on the American continent. The most notable feature, apart from their minute size, is the distinctive appearance of the larvae which seem to have developed characteristics similar to those of the limnephiloid groups in association with the possession of cylindrical cases. As Ross (1956) points out, however, it is unlikely that the Neotrichiini gave rise to the limnephiloid branch of the Trichoptera since this tribe is a very specialized member of the Hydroptilinae, the superficial similarities having arisen by parallel evolution. In addition, the larvae do not seem to have the habit of feeding on filamentous green algae, as is characteristic of the Hydroptilini, and are supposed to be detritus-feeders. From the form of the larval mandibles, which are robust and not markedly dentate or asymmetrical, the detritus-feeding habit would appear to be a primary characteristic and not secondarily derived from the algal-feeding condition (cf. *Ithytrichia*). The position of the Neotrichiini within the Hydroptilidae will be discussed later.

Genus *NEOTRICHIA* Morton

Cyllene Chambers, 1873 : 124. Type-species: *Cyllene minutissimella* Chambers, by monotypy. [Preoccupied several times, vide Fischer, 1961.]



Figs 101–107 Neotrichiini. 101, ♂ genitalia, lateral view, *Neotrichia* (vide Figs 15, 16). 102–104, *Neotrichia* sp.; (102) larva, lateral view; (103) case, lateral view; (104) head, larva, dorsal view. 105–107, *Mayatrichia ayama* Mosely; (105) head, larva, dorsal view; (106) anal proleg, larva, lateral view; (107) larval and pupal cases, lateral views.

Neotrichia Morton, 1905 : 72. Type-species: *Neotrichia collata* Morton, by monotypy.

Exitrichia Mosely, 1937 : 170. Type-species: *Exitrichia anahua* Mosely, by original designation. [Synonymized by Ross, 1944.]

Dolotrichia Mosely, 1937 : 177. Type-species: *Dolotrichia canixa* Mosely, by original designation. [Synonymized by Ross, 1944.]

Guerrotrichia Mosely, 1937 : 179. Type-species: *Guerrotrichia caxima* Mosely, by original designation. [Synonymized by Ross, 1944.]

Lorotrichia Mosely, 1937 : 181. Type-species: *Lorotrichia hiaspa* Mosely, by original designation and monotypy. [Synonymized by Ross, 1944.]

DISTRIBUTION. Nearctic, Neotropical.

Neotrichia is exclusively a New World genus with representatives occurring most abundantly in the U.S.A. and Mexico, although a few species have been recorded from Canada, the Antilles Surinam and Brazil. There are 46 species which fall into a number of distinct groups which are characterized by features of the male genitalia and which correspond with the genera described by Mosely (1937) and subsequently synonymized by Ross (1944). The Surinamese species (Flint, 1974) appear to fall into two additional groups.

According to Ross (1944) the larvae of *minutissimella*, *okopa*, *collata* and *riegeli* are known but only those of the first named have been described. However, Flint (1964; 1968b; 1968c) has since described the larva of *iridescens*.

DIAGNOSIS. *Adult*. Spur formula 0.2.3: ♂ genitalia (Fig. 101) sometimes with ventral process on sternite VIII; segment IX annular, generally complete dorsally and ventrally; tergite X variable but usually forming a well-developed dorsal plate; inferior appendages distinct, somewhat elongate, usually with prominent, spatulate bracteole (*Br*); subgenital plate well developed with a pair of apico-ventral setate lobes (representing fused bilobed process ?); a pair of narrow subgenital appendages sometimes present ('slender structure' (Flint, 1964); 'filiform appendage' (Ross, 1941b)); aedeagus elongate, generally with a wide tubular base narrowing to a median constriction or neck from which arises a stout spiral process, apical half more slender, divided at apex or bearing apical spines.

Larva (Figs 102, 104). Head cone-shaped, tapering anteriorly; labrum symmetrical; mandibles sub-symmetrical, short, robust, not markedly dentate; thoracic nota covered in long sparse setae; legs long

and slender (cf. *Mayatrichia*): abdomen cylindrical but not as rotund as in *Mayatrichia*, intersegmental grooves distinct.

Case (Fig. 103). Cylindrical, tapering posteriorly, basically of silk and often covered in small sand-grains.

BIOLOGY. Larvae found in rapid sections of rivers and streams.

Genus *MAYATRICHIA* Mosely

Mayatrichia Mosely, 1937 : 182. Type-species: *Mayatrichia ayama* Mosely, by original designation.

DISTRIBUTION. Nearctic.

There are only four species in this genus which are all of local occurrence but have an overall distribution ranging from Saskatchewan to Mexico and from Ontario to Maine. Ross (1944 : 278) gives a key to the males of the three North American species (*ayama*, *ponta* and *acuna*) with *rualda* from Mexico being described by Mosely (1937 : 183). The larvae and cases of *ayama* (including an early instar) and *ponta* have been described by Ross (1944) and Wiggins (1977) respectively.

DIAGNOSIS. *Adult.* Spur formula 0.2.4: ♂ genitalia with sternite VI with a long, slender ventral process; segment IX annular, deeply incised along postero-ventral margin, accentuated by postero-lateral processes; tergite X membranous, hood-like; inferior appendages with broad, setae-bearing posterior margin and a small, digitate, dorso-lateral projection; subgenital plate well developed with postero-medial, ventrally directed processes and produced dorso-laterally to meet tergite X; bilobed process absent; aedeagus simple, long, apex filiform or with three 'staggered tubercles' (Ross, 1944).

Larva (Figs 105, 106). Head very attenuate anteriorly: thoracic nota covered in short, stout setae; legs relatively shorter and more robust than in *Neotrichia*: abdomen rotund, cylindrical, with faint intersegmental grooves; lateral setal fringe present only in *ayama*.

Case (Fig. 107). Cylindrical, tapering posteriorly, constructed of secretion only but with strengthening transverse or longitudinal ridges.

BIOLOGY. According to Wiggins (1977) the larvae occur on rocks in rapid sections of rivers and streams, generally in rather large bodies of running water.

Tribe **HYDROPTILINI** Stephens

Hydroptilidae Stephens, 1836 : 151. Type genus: *Hydroptila* Dalman, 1819.

DISTRIBUTION. Cosmopolitan (excluding polar regions).

The Hydroptilini, as interpreted here, contains the most widely distributed and successful contemporary genera of the subfamily Hydroptilinae. Although the tribe may appear to be very heterogeneous when considering the variety of both adult and larval morphological features, habits and habitat preferences, all members do have a number of basic affinities. These include features of the adult thorax and the male genitalia, and also the fundamental association of the larvae with green filamentous algae in more slowly moving bodies of water. Owing to the diversity of the group, however, it is difficult to give a precise diagnosis of the tribe. The following is only a preliminary attempt at a formal diagnosis of the tribe, since this must await further more detailed research into the possible relationships of the genera and the discovery of all the larval stages.

DIAGNOSIS. *Adult.* Forewing length 1.5–6.0 mm. Head basically unmodified (e.g. Fig. 108); antennae simple; ocelli 3 or 0; postoccipital lobes variable, modified in *Hydroptila* (♂) as 'scent caps'; tentorium variable, distinct or reduced; shape of thoracic nota variable (Figs 108, 139); mesoscutellum without transverse suture, diamond-shaped or with convex anterior edge; metascutellum pentagonal or with convex anterior edge; spur formula 0.2.3, 0.2.4, 0.3.4 or 1.3.4: lateral setate process of abdominal segment V present, pit sometimes sculptured: ♀ genitalia (Figs 17, 121) basically a simple telescopic oviscapt, sometimes fused and non-retractile: ♂ genitalia very variable with form characteristic for each genus (Figs 109, 115, 122), aedeagus usually with spiral 'titillator'.

Larva. The larvae of *Microptila*, *Dhatrichia*, *Stenoxyethira* and *Xuthotrichia* have not yet been described. Basically of the typical hydroptilid 'purse-case' building form. Head unmodified, mouthparts usually showing various degrees of specialization associated with feeding on the cell contents of green filamentous algae; lateral line and gills absent, body often slightly compressed laterally, anal prolegs fused to sides of segment X, abdominal tergites usually absent, 'dorsal rings' present. The forms of the larva and its case

vary according to habits and habitat preferences. Substrate dwellers such as *Hydroptila* retain the generalized hydroptilid form and their 'purse-type' cases often incorporate sand-grains and diatoms, possibly to aid ballast. Larvae found amongst aquatic vegetation are usually characterized by their lighter cases, often of secretion only, and the elongation of the mid- and hindlegs. The recently described larva of *Ugandatrichia* is very specialized, being adapted for life in torrenticolous conditions. Many of its features parallel those of *Stactobia* and leucotrichiine larvae, for example, in that it is strongly dorso-ventrally flattened and heavily sclerotized, with well-developed abdominal tergites. *Ugandatrichia* is also unique in that the fifth instar larva does not build a case until just prior to pupation.

Pupa. Typically hydroptilid, mandibles long and without teeth.

DISCUSSION. The tribe Hydroptilini is considered here to consist of three subgroups which are distinguished by male and female genitalic characters and the general appearance and habits of the larvae. Within each subgroup the genera variously exhibit both generalized and specialized hydroptilid characteristics. The subgroups are defined below.

The *Agraylea*-group. This contains some of the larger and more generalized hydroptilids with respect to the overall appearance of the adults. The male genitalia, however, are rather distinctive and conform to a common basic pattern within the subgroup. The larvae of *Agraylea* are essentially adapted for life in vegetation thickets in slow-moving to static bodies of water, whereas those of *Ugandatrichia* are adapted for life in torrenticolous habitats and are free-living in the fifth instar.

The *Hydroptila*-group. This essentially consists of the nominate genus *Hydroptila* with which a number of genera have here been synonymized. The adults exhibit generalized but distinctive patterns of genitalia which vary slightly between species-groups; the larvae are basically typical of the hypothetical generalized hydroptilid but are adapted for feeding on filamentous algae on more or less exposed substrates in moderate to fast-flowing water. The genus is distinguished by the specialized cephalic (postoccipital) scent-caps of the males and the absence of ocelli in both sexes. *Hydroptila* contains the greatest number of species within the Hydroptilidae and has the widest geographical distribution; it therefore may be regarded as perhaps the most successful genus of the family.

The *Oxyethira*-group. This is a more heterogeneous group with regard to adult features, each genus possessing a very distinct set of genitalia, but it is characterized by the relatively uniform appearance of the larvae. The latter are specialized filamentous algal feeders and are generally associated with vegetation thickets in slowly moving to static bodies of water. Within the group there is a definite trend towards the elongation of the mid- and hindlegs in the larvae which reaches its extreme condition in *Tricholeiochiton fagesii*. *Oxyethira*, like *Hydroptila*, has a continuous world-wide distribution (although represented by fewer species) while *Stenoxyethira*, *Paroxyethira* and *Xuthotrichia* are restricted to SE. Asia, New Zealand and Australia respectively; *Tricholeiochiton* has one west Palaearctic and two SE. Asian representatives only.

Thus the Hydroptilini as interpreted here consists of three distinct and more or less specialized groups which have been united on the basis of the form of the male aedeagus and the basic associations of the larval stages with green filamentous algae. The three groups probably diverged relatively early in the evolution of the Hydroptilini branch although somewhat later than the Ochrotrichiini, Neotrichiini and Orthotrichiini split off from this main stem (*vide* Chart II). The hypothetical ancestral Hydroptilini larva probably differed little in appearance from that of the present-day generalized condition as seen, for example, in *Hydroptila*, with the slightly laterally compressed abdomen, subequal legs and simple 'purse-type' case. Such a condition is also seen in the unspecialized members of other groups such as the Ptilocolepinae, *Stactobiella*, *Ochrotrichia* and *Dibusa*. Within the Hydroptilini, however, the form of the larval case varies little from the generalized condition in *Agraylea*, *Allotrichia*, *Hydroptila*, *Tricholeiochiton*, *Paroxyethira* and perhaps *Xuthotrichia*, the only specialized genus in this respect being *Oxyethira* with its distinct 'jug-shaped' cases. The main differences in case-form appear to be associated with corresponding differences in larval morphology which reflect trends towards adaptation to life in vegetation thickets in slow-moving bodies of water. Thus the cases lose any extraneous particles which might weigh them down and the larvae tend to have longer mid- and hindlegs.

Within the *Agraylea*-group, *Agraylea* and *Allotrichia* have a temperate (to cool temperate)

distribution, *Dhatrichia* and *Microptila* are more subtropical (to temperate) while *Ugandatrichia* is tropical. *Hydroptila* and *Oxyethira* are cosmopolitan genera and occur throughout the Americas and through SE. Asia and Indonesia to the Australian region. The endemic Australian and New Zealand genera, *Xuthotrichia* and *Paroxyethira* respectively, probably represent descendants of an early branch of the *Oxyethira*-line which occurred in the Australian region but which was cut off from the mainland leaving the two genera to evolve in isolation ever since. *Tricholeiochiton* is distinguished by its rather unusual distribution pattern with one western Palaearctic species and two SE. Asian species. The origins of this genus are obscure but, from the general form of the larva, it may again have been derived from an early offshoot of the *Oxyethira*-line.

The success of the Hydroptilini (in terms of its present-day distribution and numbers) may be due partly to its larval associations with green filamentous algae and partly to its tolerance of a wider range of aquatic habitats in comparison with the more specialized Stactobiini and Leuco-trichiini and the more restricted Ochrotrichiini and Neotrichiini. The utilization of algal filaments (i.e. their cell fluid contents) may have opened the pathway from a life restricted to rocky and stony substrates, which is maintained to a certain extent in *Hydroptila*, to one in vegetation thickets. The latter may have at first been restricted to the banks of streams and larger, moderately flowing rivers but thence radiated into the more slowly moving waters of backwaters, lakes and ponds culminating in artificial, almost static, bodies of water such as reservoirs, etc. The distribution of vegetation-dwellers, or rather their dispersal, may also be enhanced by the accidental transport of the immature stages with the aquatic plants on which they dwell; here again the influence of man may play an important part in the success of these insects. *Hydroptila* shows great species variation as to habitat preference (as does *Oxyethira* to a certain extent); some, such as *forcipata* and *angulata* in Britain, favour the more stony fast-flowing streams of the north and west uplands while others, such as *sparsa* and *simulans*, occur more frequently in the slower and relatively more vegetated streams and canals of the lower regions.

Recent discovery of the larva of *Ugandatrichia* (Scott, 1976) indicates that this genus may have branched off from the Hydroptilini line at a very early stage in the evolution of the group, the larvae becoming specialized tropical members of the hydropetric fauna while the adults retained the generalized primitive form as seen also in *Agraylea*, for example.

In conclusion the Hydroptilini, although superficially seeming to be a somewhat heterogeneous tribe, can be seen to have a relatively recent point of origin along the main Hydroptilinae branch (although this was still geologically quite distant as indicated by the very modern looking fossil amber species of *Agraylea* and *Allotrichia*). The group has radiated out to fill a number of aquatic niches in association with green filamentous algae and larger and more slowly moving bodies of water. Early offshoots of the Hydroptilini-line may have given rise to the Ochrotrichiini and Neotrichiini in the Americas (and the unique, red-alga associated, Nearctic genus *Dibusa*) and the highly specialized Orthotrichiini (q.v.).

Genus *AGRAYLEA* Curtis

Agraylea Curtis, 1834 : 217. Type-species: *Agraylea sexmaculata* Curtis, by subsequent designation by Westwood, 1840.

Agraules Agassiz, 1846 : 32. [Unjustified emendation of *Agraylea* according to Fischer, 1961.]

Hydrorchestria Kolenati, 1848 : 103. Type-species: *Agraylea sexmaculata* Curtis, by subsequent designation by Kimmins, 1950. [Synonymized by Kimmins, 1950.]

DISTRIBUTION. Holarctic.

There are nine species in this small Holarctic genus although some of these are of doubtful status and are very restricted in occurrence. The most successful species are *sexmaculata*, which has a wide western Palaearctic distribution, and *multipunctata*, which is reputedly Holarctic but which probably involves a species complex. In my opinion the Nearctic form of *multipunctata*, as figured in Ross (1944), is distinct from the Palaearctic form (the type) in features of both the male and female genitalia (notably the relative size and shape of the inferior appendages and ventral process of sternite VII of the male) and should be referred to by its original designation (*signata* Banks). However, Ross (*in litt.*) has Alaskan material of what may prove to be a third species and he agrees that a thorough study should be made of all records previously referable to *multipunctata*.

from throughout the Holarctic region, including the records of the closely related European species, *cognatella*.

The following list summarizes the status of the species at present comprising the genus *Agraylea*.
A. spathifera Ulmer: Baltic Amber; closely related to *multipunctata*.

A. insularis Hagen: known only from a single female specimen (now lost) from Madeira which, according to Nybom (1948), was probably a female of *Stactobia atra* (Hagen).

A. drosima Navás: Navás (1917) gives only a crude description and figure of this subsequently unrecorded species from Spain; its identity remains doubtful until the type-specimen can be located.

A. argyricola Kolenati: originally described from Sweden and subsequently from Finland, this species has been regarded of doubtful identity ever since Eaton (1873) considered it to be a possible synonym of *multipunctata*; Nybom (1960) regards it as an 'unintelligible species' and has withdrawn it from the Finnish list.

A. multipunctata Curtis: possibly represented by a species complex (see above) consisting of *multipunctata* Curtis (Palearctic) and *multipunctata* Curtis sensu Morton (1905) (Nearctic) (= *signata* Banks ?).

A. sexmaculata Curtis: a distinct Palearctic species.

A. cognatella McLachlan: in this species the abdomen of the type-specimen, which has been crudely figured by McLachlan (1880), has been lost; however, it appears to be most closely related to *multipunctata*; the larva has been described by Solem (1972), although he had no spare adult specimens available for examination.

A. saltesea Ross: Nearctic (Montana, California); according to Ross (1944) this bears most resemblance to *multipunctata*.

A. costello Ross: Nearctic (Ontario, Maine); Ross (1941a) considers this to be most closely related to *Allotrichia pallicornis* (Eaton) (q.v.).

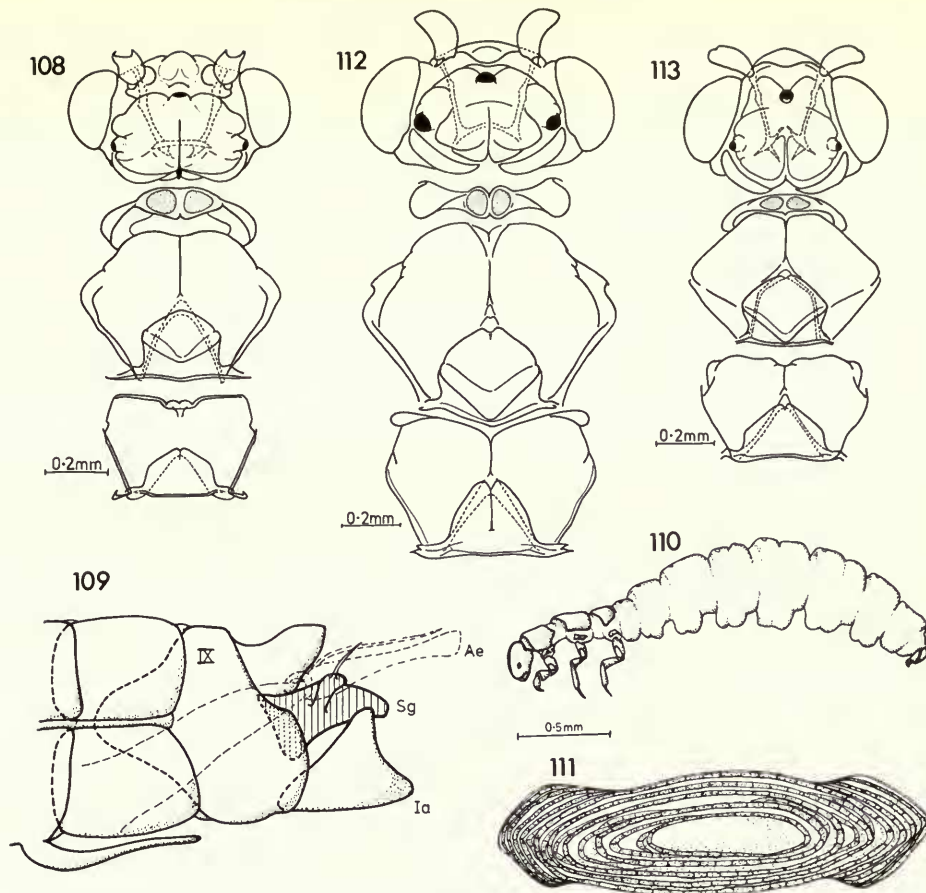
The larvae of the following species have been described: *multipunctata* (Nielsen, 1948; Lepneva, 1964; Hickin, 1967); *sexmaculata* (Lepneva, 1964; Barnard, 1971) and *cognatella* (Solem, 1972).

Agraylea is most closely allied morphologically to *Allotrichia* from which it was originally distinguished by the presence of fork 1 (R_2 and R_3) in the hindwing of *Agraylea*. This has not proved to be a consistent generic feature and the genera may later be found to be synonymous. They have been treated separately in this account, however, because the male genitalia of the *Allotrichia*-group of species conform to a distinct pattern (which may, nevertheless, be derived from the basic *Agraylea* plan). Also, the form of the male genitalia appears to link *Agraylea* with *Ugandatrichia* (and *Moselyella*) and *Dhatrichia*, the relationships of which will be discussed later.

The following diagnosis is based on specific descriptions and examination of adult and larval material in the BMNH collections. The general morphological features, apart from those of the genitalia, also apply to *Allotrichia*.

DIAGNOSIS. *Adult.* Forewing length 4–5 mm; wings (Fig. 7) relatively broad, apices slightly tapered, venation fairly complete (cf. Figs 5 and 8): head (Fig. 108) and antennae simple; ocelli 3; postoccipital lobes unmodified; tentorium distinct; mesoscutellum (Fig. 108) narrow, diamond-shaped; metascutellum narrow, pentagonal, parallel-sided: spur formula 0.3.4: lateral setate processes of abdominal segment V present, typical: ♀ genitalia a simple oviscap: ♂ genitalia (Fig. 109) generally with a long ventral process on segment VIII; segment IX forming an annulus, usually with a deep dorso-anal indentation; tergite X reduced to a short membranous lobe; inferior appendages generally well developed; subgenital plate triangular, tapering posteriorly (ventral view) and with a median, ventrally projecting process; aedeagus relatively short and stout with distinct proximal and distal halves, proximal broad ejaculatory duct giving rise to the slender distal intromittent organ from which arises the spiral 'titillator' (midway between the end of the ejaculatory duct and the constriction at the base of the intromittent organ).

Larva (Fig. 110). Body slightly compressed laterally: dorsal ecdysial lines of head indistinct; labrum symmetrical, short and broad with convex sides, concave anterior margin and small, antero-lateral projections; mandibles asymmetrical, robust (left with apical tooth and projecting dorsal blade without teeth but with small apical denticles, median brush present; right mandible without teeth which are replaced distally by two tubercles, inner median margin with central membranous bladder-like structure); 'postmental sclerites' entire in *multipunctata*, paired in *sexmaculata* (Figs 22, 21); posterior ventral apotome absent: legs short, subequal; fore-femur short and broad, baso-ventrally produced into a short



Figs 108–113 Hydroptilini, *Agraylea*-group. 108, 112, 113, head and thorax, dorsal view; (108) *Agraylea*; (112) *Ugandatrichia* (*Moselyella*); (113) *Ugandatrichia* s.str. 109, generalized ♂ genitalia, lateral view, *Allotruchia* (vide Figs 15, 16). 110–111, *Agraylea* sp., lateral view; (110) larva; (111) case.

process with apico-ventral projection of trochanter; distal process of tibia with typical spinose setae; small oral sternite present on prothorax only (Fig. 40); abdominal segment I larger than metathorax, abdomen widest at segment IV, intersegmental constrictions deep; dorsal 'rings' present on segments II–VIII; tergite present on segment IX; anal prolegs fused to X, anal claws relatively longer than in other hydroptilids. The early instars are described by Nielsen (1948).

The larvae of *multipunctata*, *sexmaculata* and *cognatella* can be distinguished by the markings of the dorsal head capsule (Solem, 1972).

Case (Fig. 111). 'Purse-type', constructed of silk and filaments of algae. The case building behaviour of *multipunctata* is described by Nielsen (1948).

Pupa. Typically hydroptilid, mandibles long, without median teeth; case a sealed larval case attached at each corner by a short silken pad to the surrounding vegetation.

BIOLOGY. The larvae of *Agraylea* occur in plant thickets in lakes and slowly flowing rivers in association with green filamentous algae. The larvae of *multipunctata* and *sexmaculata* have been observed to feed (Nielsen, 1948; Barnard, 1971) by grasping each algal filament with their modified chelate forelegs and passing it upwards between the mandibles with which they bite into each cell; the cell contents are then sucked out through this excision. According to Wiggins (1977) gut contents of *multipunctata* (Nearctic) included diatoms while Siltala (1907) records *Fucus*, algae and diatoms from the guts of Palaearctic specimens of this species.

Genus *ALLOTRICHIA* McLachlan

Allotrichia McLachlan, 1880 : 508. Type-species: *Agraylea pallicornis* Eaton, by monotypy.

DISTRIBUTION. Palaearctic (including N. Africa).

This genus was erected for a single male specimen of what McLachlan regarded as a new species from Worcester, England but, just prior to publication, he discovered that it was identical to *Agraylea pallicornis* Eaton which thus became the type-species. McLachlan regarded the genus as distinct from *Agraylea* on the basis of the absence of fork 1 (R_2 and R_3) (vide Fig. 7, arrowed) in the hindwing. As pointed out previously, this has not proved to be a constant diagnostic feature and the genera may later come to be regarded as synonyms. *Allotrichia* is retained here, however, as the male genitalia of the constituent species conform to a characteristic pattern and the female genitalia and larval habits of *pallicornis* are distinct from those of *Agraylea* (although it is not certain whether *pallicornis* is typical of the *Allotrichia* group in general).

Apart from *pallicornis*, which has a widespread western Palaearctic distribution, the other members of this genus are all very local in occurrence; the following list summarizes the distribution and status of the species of *Allotrichia*.

A. ampullata Ulmer: Baltic Amber.

A. succinica Hagen: Baltic Amber.

A. heterocera Navás: based on a single female specimen from Spain with a vague description accompanied by a very nondescript figure and said by Navás to 'resemble *pallicornis*'; this species is therefore unrecognizable and must await the discovery and examination of the type.

A. pallicornis (Eaton): central and southern Europe, Algeria, Iran.

A. vilnensis Raciecka: refigured by Schmid (1959a) and known from the type-specimen from Poland and further material from Iran (Schmid); this species is distinct but very closely related to *pallicornis*.

A. tauri Jacquemart: described from a single male specimen from Turkey; it may prove to be synonymous with *pallicornis*.

A. teldanica Botosaneanu: a distinct species from Israel, closely related to *vilnensis*.

A. laerma Malicky: a distinct species from Greece.

[*A. africana* Marlier & Vaillant: I believe this species from the Congo to belong to the genus *Ugandatrichia* and to be closely related to, if not synonymous with, *U. nigra* Mosely (q.v.).]

The members of the genus *Allotrichia* are morphologically very similar to those of *Agraylea* and the adult generic diagnosis given for the latter, excluding the male and female genitalia, also applies to *Allotrichia* and therefore has not been repeated here. New species are allocated to either genus not according to the fusion of R_2 and R_3 in the hindwings, as was previously the practice, but by the general form of the male genitalia. However, Ross (1941a) states that the genitalia of *Agraylea costello* Ross are more like those of *Allotrichia pallicornis*, thus implying that the two genera are synonymous. Before any definite conclusions can be drawn, however, a thorough study of the *Agraylea*-*Allotrichia* complex needs to be carried out, incorporating as many male, female and larval features as possible; only the larva of *pallicornis* has so far been described (Giudicelli & Vaillant, 1967).

The following accounts of the male and female genitalia and the immature stages are based on original descriptions and examination of adult material of *pallicornis* in the BMNH collections.

DIAGNOSIS (see also *Agraylea*). *Adult*. ♀ genitalia an oviscapt; segment VIII without a ventral sclerite but with a characteristic asymmetrical groove. ♂ genitalia (Fig. 109) with concave inferior appendages, broad with concave posterior margins; the subgenital plate bears a pair of characteristic asymmetrical dorsal processes.

Larva (cf. Fig. 110) (after Giudicelli & Vaillant, 1967). Characterized by the lightness of the pigmentation of the sclerites and absence of dorsal markings (cf. *Agraylea*): setae of head and labrum much shorter than in *Agraylea*; dorsal ecdysial lines of head appear to be more distinct than in *Agraylea*; mandibles similar to those of *Agraylea* although the apices are more dentate; foreleg with distinctive chelate form but devoid of the specialized distal process of the tibia; abdominal tergites absent, including tergite IX (unusual); anal prolegs simple, claws apparently short.

Case. Identical with that of *Agraylea* (cf. Fig. 111).

Pupa. Typical; mandibles long with fine serrations along inner edge; case similar to that of larva but sealed, with two attachment pedicels (cf. four in *Agraylea*) at either end of one long side by which the case is held vertical to the substrate.

BIOLOGY. The immature stages were found in a rapid stream at 750 m with little shelter or marginal vegetation. Larval gut contents revealed, according to Giudicelli & Vaillant (1967), that the larvae are secondary substrate feeders which have been derived from the basic filamentous algal-feeding *Agraylea* stock; they have retained certain features associated with algal-feeding such as the asymmetrical mandibles, chelate forelegs, lateral flattening of the body and case and the incorporation of algal filaments into the latter.

The larvae of *Allotrichia pallicornis* thus differ from those of the known species of *Agraylea* in the lack of pigmentation, absence of abdominal tergite IX, simplicity of the anal prolegs, shorter head and labral setae, dentate mandibles and the attachment of the pupal case by two (cf. four) adhesive discs. These differences are apparently due to structural adaptations to living in fast-flowing water conditions and detritivorous feeding habits. As only the larva of *pallicornis* has so far been described, it is not known whether these features are diagnostic of *Allotrichia* species in general.

Genus *MICROPTILA* Ris

Microptila Ris, 1897 : 416. Type-species: *Microptila minutissima* Ris, by monotypy.

DISTRIBUTION. W. Palaearctic.

Microptila was erected for a new Swiss species, *minutissima* and *bejela* Mosely was subsequently described from Southern Yemen (Aden). Schmid (1960), as a result of studies on the trichopterous fauna of Sri Lanka and Pakistan, synonymized the African genus *Ugandatrichia* Mosely and the SE. Asian genus *Moselyella* Kimmins with *Microptila* on the basis of features of the wing venation and the general form of the male genitalia. Schmid described a number of new species, mainly from Pakistan and adjacent areas, which he considered to exhibit male genitalic features intermediate between those of the *Ugandatrichia*-*Moselyella* complex, which contains some of the largest known hydroptilids, and *Microptila*, which contains some of the smallest.

I have examined type-material of all three genera (BMNH collections) (including paratypes of three species described by Schmid (1960) and placed in *Microptila* sensu Schmid) but only one specimen of the type-species, *minutissima*, of *Microptila* was available for study. This is mounted in Canada Balsam and is now in a very poor condition, the features of the genitalia (male) being indistinct and the thorax completely destroyed thus rendering a comparative study impossible. Nevertheless, *Ugandatrichia* and *Moselyella* are considered to be distinct from *Microptila* s.str., the two former genera comprising a distinct group which has more affinities, at least in the adult stages, with *Agraylea* and *Allotrichia*, whereas *Microptila* s.str. bears more resemblance to *Dhatrichia* Mosely. This raises the problem of the correct generic identity of the species described by Schmid as *Microptila* s.l., which will be dealt with below.

On the basis of adult features alone, I propose to reinstate the genus *Ugandatrichia*, with *Moselyella* as a junior synonym, and to interpret *Microptila* in its original sense. These views may need to be modified with the discovery of new species and the larval stages, which have so far been described only for *Ugandatrichia*.

DIAGNOSIS. *Adult*. Forewing length 1.5–3.0 mm; antennae 20- to 25-segmented; ocelli 3: mesoscutellum short, anterior margin convex; metascutellum trapezoidal: spur formula 0.3.4: ♀ genitalia an oviscapt: ♂ genitalia simple; segment IX large, fused, with a shallow excision along dorso-posterior margin; tergite X forming a short membranous dorsal lobe; subgenital appendages elongate, slender, apparently arising lateral to tergite X; inferior appendages elongate, apices slightly incurved; subgenital plate elongate, semi-tubular; aedeagus simple, long and slender, tapering to a pointed apex in *bejela* (vide Mosely, 1948) and with a short spiral 'titillator' in *indra* and *apsara*.

M. indra is retained in this genus on the basis of the form of the thoracic nota; *apsara* is only doubtfully retained.

Genus *UGANDATRICHIA* Mosely gen. rev.

Ugandatrichia Mosely, 1939b : 36. Type-species: *Ugandatrichia minor* Mosely, by original designation. *Moselyella* Kimmins, 1951 : 195. Type-species: *Ithytrichia violacea* Morton, by original designation and monotypy. [Synonymized by Schmid, 1960.]

DISTRIBUTION. Africa (Congo, Uganda, Kenya, Zimbabwe); S. and SE. Asia (Burma, Assam, Pakistan, Sri Lanka, Sarawak).

Ugandatrichia is a small genus (10 species) of large, primitive-looking tropical hydroptilids. Schmid (1960) synonymized the then distinct genera *Ugandatrichia* and *Moselyella* with the Palaearctic genus *Microptila* but, for the reasons set out in the discussion below, *Ugandatrichia* (including *Moselyella*) has here been reinstated.

The following diagnoses are based on examination of adult material in the BMNH collections and on Scott's (1976) descriptions of the adults, pupae and larvae of *rhodesiensis*.

DIAGNOSIS. *Adult*. Forewing length variable, 2–6 mm; wings relatively broad but still long and acuminate as typical of the Hydroptilinae; forewings with dense setal covering (dark) with an oval patch of creamy scale-like hairs arising centrally from the membrane in *cyanotrichia* (Kimmins) (Fig. 6): tentorium complete (Figs 112, 113); antennae usually long (32–37 segments); ocelli 3: mesoscutellum diamond-shaped (Figs 112, 113) as in *Agraylea* (Fig. 108); metascutellum 'convexly subtriangular', narrow: spur formula 0.3.4: *violacea*, *cyanotrichia* and *nikitaruwa* (Schmid) each has a pair of long, membranous extrusible processes arising laterally between the tergite and sternite of segment II in the male: ♀ genitalia an oviscap; sternite VII with diagnostic patch or row of setae in certain species; sternite VIII with process or some other distinctive marking: ♂ genitalia with segment IX well developed, variously with dorsal and ventral posterior and anterior excisions; tergite X a median lobe with well-developed elongate lateral processes; inferior appendages large, broad and elongate; subgenital plate trilobed (or emarginate); aedeagus with distinct proximal and distal regions, divided by a constriction adjacent to which arises a short, spiral 'tillator'.

The thoraces of *nikitaruwa* (Schmid) and *sourya* (Schmid) are almost identical to that of *Ugandatrichia* (as seen in species of *Moselyella*), while *roudra* (Schmid) is included here on the basis of size and male genitalic affinities with *Ugandatrichia* species as noted by Schmid (1960). *M. apsara* Schmid may also belong here (see *Microptila* s.str. section).

Larva. The larva of *U. rhodesiensis* Scott has recently been described by Scott (1976) from which the following description of the immature stages and biology has been taken (for figures see Scott, 1976).

Fifth instar free-living, robust and heavily sclerotized, flattened dorso-ventrally: head relatively small, oval, tapering anteriorly; eyes large, distinct; ecdysial lines distinct; antennae well developed; anterior and posterior ventral apotomes small, former very narrow with long, slender anterior arms; labrum well developed, rectanguloid with convex sides, convex anterior margin and dense setal brushes arising postero-ventrally and projecting beyond anterior margin; mandibles almost symmetrical, apices blunt with no lateral teeth, left with dense inner brush of predominantly feathered spines ('penicillus'), right ridged externally and with long inner feathered spine and tuft of shorter bifid spines: all three thoracic nota paired; pleurites with preepisternite, episternite and epimeron; sterna entirely membranous and strongly muscular; legs short, stout and serving as powerful clinging appendages: abdomen dorso-ventrally flattened, gills absent; well-sclerotized tergites present dorsally on all segments, each with clear central spot on segments I–VIII; tergite IX with emarginate posterior margin; all segments distinctly demarcated and strongly muscular, ventral surfaces of segments II–VIII each with a pair of suckers close to lateral margins (adaptation for clinging to rocks); anal prolegs short, stout, fused to X and with simple large, hooked anal claws.

The larval stages are free-living throughout, a case being built only at the end of the final instar in which the latter pupates.

Pupa. Typically hydroptilid. Pupal case sac-like, tubular but not flattened and anchored by a holdfast at one end; case of tough, semi-transparent, parchment-like secretion.

BIOLOGY. The larvae and pupae of *rhodesiensis* were collected mainly from the most torrential parts of the waterfall on the Bundi River in Rhodesia. The larvae are clearly adapted for living in such harsh hydropetric conditions as indicated by their strongly sclerotized, robust, dorso-ventrally flattened form, clinging appendages and loss of the case building habit in the final instar. The form of the labrum and mandibles suggests that the larvae are substrate feeders.

DISCUSSION. According to the basic form of the male genitalia and the structure of the thoracic nota, especially with regard to the characteristic diamond-shaped mesoscutellum, I consider

Ugandatrichia and *Moselyella* to be synonymous and closely related to *Agraylea* as apposed to *Microptila* in which the mesoscutellum is more 'kite-shaped' with a convex anterior margin. Only specimens of *nikitaruwa* (Schmid), *sourya* (Schmid) and *indra* Schmid were available for study (BMNH collection, paratypes) and, from their thoracic features, the last mentioned would appear to belong to *Microptila* s.str. while the other two strongly resemble *Ugandatrichia* species. The affinities of *apsara* (Schmid) and *roudra* (Schmid) are still doubtful.

Thoracic structure alone, however, cannot be used as an indication of generic affinity. As Schmid (1960) rightly states, the genitalia of the *Microptila*-*Ugandatrichia*-*Moselyella* complex do have a common basic form but this is very generalized and has certain features in common with the genitalia of *Agraylea*, *Allotrichia* and *Dhatrichia*. Indeed, *Allotrichia africana* Marlier & Jacquemart appears to belong to *Ugandatrichia* and is very close to, if not synonymous with, *U. nigra* Mosely. Contrary to Schmid (1960), it is unlikely that there is any relationship between *Microptila* s.l. and the Nearctic-Neotropical subgenus *Ochrotrichia* (*Metrichia*) since the genitalia of the two groups are quite distinct and the characteristic mesoscutellar suture of *Ochrotrichia* is absent in *Microptila*.

Due to the recent description of the immature stages of *rhodesiensis* by Scott (1976), I have been able to include the following remarks concerning the affinities of the larvae with those of other hydroptilid genera. As Scott notes, the only other hydroptilid genus to retain the free-living habit throughout its larval existence is the Central American genus *Alisotrichia*. The larvae appear to have developed parallel structural adaptations suiting them for life in torrenticolous conditions but, as can be seen from a comparison of basic larval and, especially, adult features, the genera are totally unrelated, any affinities being purely superficial. *Alisotrichia* is a distinct, though rather isolated, member of the exclusively New World Leucotrichiini whereas *Ugandatrichia* would appear to be a distinct Palaeotropical component of the Hydroptilini.

The structural modifications of *Ugandatrichia* larvae are also paralleled to some extent by those of *Stactobia*, which are also heavily sclerotized, dorso-ventrally flattened with robust clinging appendages and similar madicolous habits. Fundamental differences can be seen, for example, in the fusion of the ecdysial lines of the head, the crenellated posterior margin of tergite IX and the retention of a case in the final instar of *Stactobia*. Comparison of the adult stages will immediately discount any close affinity between the two genera. It is interesting to note here that *Ugandatrichia* is essentially Palaeotropical whereas *Stactobia* is principally Palaearctic.

The discovery of the larva of *Ugandatrichia* does not, unfortunately, shed any light on its true generic affinities as may have been hoped since, as has been emphasized throughout this account, it is highly specialized and possesses structural modifications which tend to mask fundamental characters. It is, however, still possible that *Ugandatrichia* may be a descendant of an early ancestor of the Hydroptilini line which spread throughout the Palaeotropical regions, the larvae becoming specialized while the adults retained the primitive generalized form similar to that seen in *Agraylea* for example.

It would now seem essential to discover the immature stages of the SE. Asian *Moselyella* group of *Ugandatrichia*, as well as those of the Palaearctic *Microptila* group to establish the true affinities of this generic complex, since basic larval forms seem to serve as useful generic indicators in the Hydroptilidae.

A single specimen (♂) of *Ugandatrichia* (*Moselyella* group) has recently been collected from Sarawak, 1978 (J. E. Marshall), BMNH coll.

Genus *DHATRICHIA* Mosely

Dhatrichia Mosely, 1948 : 78. Type-species: *Dhatrichia inasa* Mosely, by original designation and monotypy.

DISTRIBUTION. Yemen, Zaire.

This small genus was first described for a single male specimen from the Yemen which is now mounted as a microscope slide preparation in the BMNH collection. A new species from Zaire, *bipunctata*, has been described by Statzner (1977), paratypes of which have been donated to the BMNH. The immature stages are unknown.

The following generic diagnosis is based on examination of the above material.

DIAGNOSIS. *Adult.* Forewing length 2 mm; wings narrow, tapering: tentorium complete but very fine medially; ocelli 3; antennae 19-segmented (male *inasa*); postoccipital lobes ovoid: mesoscutellum with convex anterior margin; metascutellum pentagonal, sides convergent anteriorly; spur formula 0.3.4: typical lateral setate processes of abdominal segment V present: ♀ genitalia an oviscapt: ♂ genitalia with segment IX annular, dorsally reduced to a narrow chitinated band and with well-developed postero-lateral sides (almost concealing genitalia in lateral view); tergite X ('upper penis cover' (Mosely, 1948)) broad, bilobed in *inasa*; inferior appendages short, apically broad, trilobed in *inasa*; subgenital plate an elongate flat process with a pair of apical setae and not extending beyond the sides of IX; aedeagus with a broad proximal ejaculatory duct and slender distal intromittent organ and with a spiral 'titillator' arising mid-length adjacent to the median constriction.

DISCUSSION. From the structure of the male aedeagus and the thoracic nota, *Dhatrichia* would appear to be a member of the Hydroptilini. The form of the male genitalia indicates an affinity with *Agraylea*, especially in the shape of segment IX and the form of the aedeagus; however, the thorax bears more resemblance to that of *Microptila* s.str. and these two genera (i.e. *Microptila* and *Dhatrichia*) can be separated in the generic key only by the form of the male genitalia.

Genus *HYDROPTILA* Dalman

Hydroptila Dalman, 1819 : 125. Type-species: *Hydroptila tineoides* Dalman, by monotypy.

Phrixocoma Eaton, 1873 : 132. Type-species: *Hydroptila sparsa* Curtis, by original designation. [Synonymized by McLachlan, 1880.]

Hydropneuma Enderlein, 1929 : 232. Type-species: *Hydropneuma juba* Enderlein, by original designation and monotypy. [Synonymized by Nybom, 1963.]

Hydroptilina Martynov, 1934 : 144. Type-species: *Hydroptilina angustipennis* Martynov, by monotypy. [Synonymized by Fischer, 1971.]

Oxydroptila Martynov, 1935 : 114. Type-species: *Oxydroptila furcata* Martynov, by original designation and monotypy. **Syn. n.**

Oeceotrichia Ulmer, 1951 : 85. Type-species: *Oeceotrichia elongata* Ulmer, by original designation and monotypy. **Syn. n.**

Pasirotichia Ulmer, 1951 : 90. Type-species: *Pasirotichia crenata* Ulmer, by original designation and monotypy. **Syn. n.**

Sumatranotrichia Ulmer, 1951 : 87. Type-species: *Sumatranotrichia trullata* Ulmer, by original designation and monotypy. **Syn. n.**

DISTRIBUTION. Cosmopolitan (excluding polar regions).

Hydroptila is the most successful genus of the Hydroptilidae with over 150 species and with an almost world-wide distribution; species have been recorded from Lapland and the northern U.S.S.R. to South Africa and Australia (including Tasmania) in the 'Old World' and throughout the Americas as far south as Nova Teutonia in Brazil. A number of geographically more or less distinct species-groups may be recognized by the forms of the male and female genitalia, and may eventually come to be considered as distinct subgenera. However, the species all have the following features in common: basic genitalia patterns; thoracic nota; absence of ocelli and presence of male dorsal postoccipital scent-organs in the adults, and the general appearance of the larvae and their cases. The immature stages are difficult to identify at the species level; Ross (1944) gives head and thoracic pigmentation patterns as rough guides to the identity of some Nearctic species although these tend to be very variable intraspecifically. My own observations indicate the possible use of features of the sculpturing and shape of the mandibles as specific guides but a full investigation was not carried out. The only satisfactory means of identification is by association with correctly identified pupae and adults.

There is no single comprehensive work on the genus as a whole, any one species-group or any particular faunal group, nor is there a key to the species of *Hydroptila*, identification at present relying on faunal keys (of which there are few) and reference to original descriptions, some of which are unsatisfactory and in need of redefinition. A species key was beyond the scope of this project but I have attempted to indicate the main species-groups, these groupings being based on affinities suggested by the original authors and, in many instances, by my own observations.

DIAGNOSIS. *Adult* (Fig. 1). Forewing length 3–4 mm: head (Fig. 114) with tentorium reduced medially; ocelli 0; antennae c. 30-segmented: mesoscutellum (Fig. 114) subtriangular with convex anterior margin; metascutellum pentagonal to triangular, anterior margin strongly convex: spur formula 0.2.4: setate processes present on abdominal segment V: ♀ genitalia a simple oviscap (Fig. 17); sternite VIII ('ventral plate', *vp*) and small sternite/s on IX ('dorsal plate/s', *dp*) sometimes present: ♂ genitalia (Figs 115–117) distinctive for each species-group but basically as follows – sternite VII often with ventral process; segment VIII rarely with ventral process; segment IX fused, annular, sometimes with antero-lateral apodemes (Fig. 117) and often with postero-lateral processes; inferior appendages distinct, usually simple, straight and elongate, sometimes modified (Fig. 117); tergite X forming a variable 'dorsal plate'; subgenital appendages variable (= 'parameres', 'lateral penis sheaths', 'intermediate appendages'); subgenital plate simple, broad, slightly emarginate in the *sparsa*- and *consimilis*-groups but absent or inconspicuous in others; bilobed process apparently absent (but may be incorporated into subgenital plate); aedeagus with distinct proximal and distal ejaculatory duct and intromittent organ respectively and a well developed spiral 'titillator'.

Larva (Fig. 118). The following species have been described (* indicates material examined in BMNH collections): *H. acuta* (Jacquemart & Coineau, 1962); *ajax*, *albicornis*, *angusta*, *armata* (Ross, 1944); *capensis* (Barnard, 1934); *consimilis* (Ross, 1944); *delineata* (Sibley, 1926); *emarginata* (Lepneva, 1932); *forcipata** (Fahy, 1972); *grandiosa*, *hamata* (Ross, 1944); *martorelli* (Flint, 1964); *pulchricornis* (Lepneva, 1964); *sparsa** (Hanna, 1961; Lepneva, 1964; Hickin, 1967); *spatulata* (Ross, 1944); *taurica* (Botosaneanu & Sykora, 1963); *tineoides** (Nielsen, 1948; Lepneva, 1964; Hickin, 1967); *trilobata* (Jacquemart, 1965); *vectis** (Jacquemart & Coineau, 1962; Lepneva, 1964); *waubesiana* (Ross, 1944).

Head elongate with almost parallel sides, almost circular in cross-section; ecdysial lines indistinct; 'postmental' sclerites (Fig. 26) fused, although a faint median line may sometimes be detected, crescentic, without posterior process (cf. *Agraylea*); labrum long, anterior margin deeply indented, lateral lobes slightly asymmetrical, row of setae anteriorly; mandibles asymmetrical (Fig. 31), form variable between species, median brush in left only: thoracic pleurites as in *Agraylea* (cf. Fig. 35) but with preepisternite free on prothorax only; single oral and paired anal sternites on prothorax only (Fig. 39); legs short, subequal (Fig. 33) with distal ventral process of fore-tibia well developed and armed with specialized setae (Fig. 47) as in *Agraylea*: abdomen typically distended; dorsal 'rings' present on segments I–VIII; tergites absent except on IX; anal prolegs fused to X; three filamentous caudal gills present (Figs 48, 49).

Case (Fig. 119). 'Purse-type', laterally compressed, constructed of silk and covered in fine sand-grains and other inorganic particles and occasionally with diatoms and algal filaments.

Pupa (Fig. 52). Typically hydroptilid, mandibles long, without teeth; pupal case simply a sealed larval case, attached to substrate by anterior and posterior adhesive discs on ventral edge, held vertically.

BIOLOGY. The larvae prefer running water in lakes, streams and rivers, usually on the bottom substrate in association with the green filamentous algae on which they feed. According to Nielsen (1948) the typical habitat of *tineoides* is that of 'stony brooks in shallow water of lakes' while others tend to prefer swifter flowing water and I agree with his observation that this is probably due to true species preferences, as distinct differences have been observed in the habitats of the British species.

Life-cycles are very variable according to species and locality; both univoltine and bivoltine species have been observed. The larvae feed on filamentous green algae by grasping the filament with the modified chelate forelegs, biting into each cell and sucking out the fluid contents.

SPECIES-GROUPS (for species see checklist). The *sparsa*-group: a very large Palaearctic group recognized by the form of the male genitalia (Fig. 115).

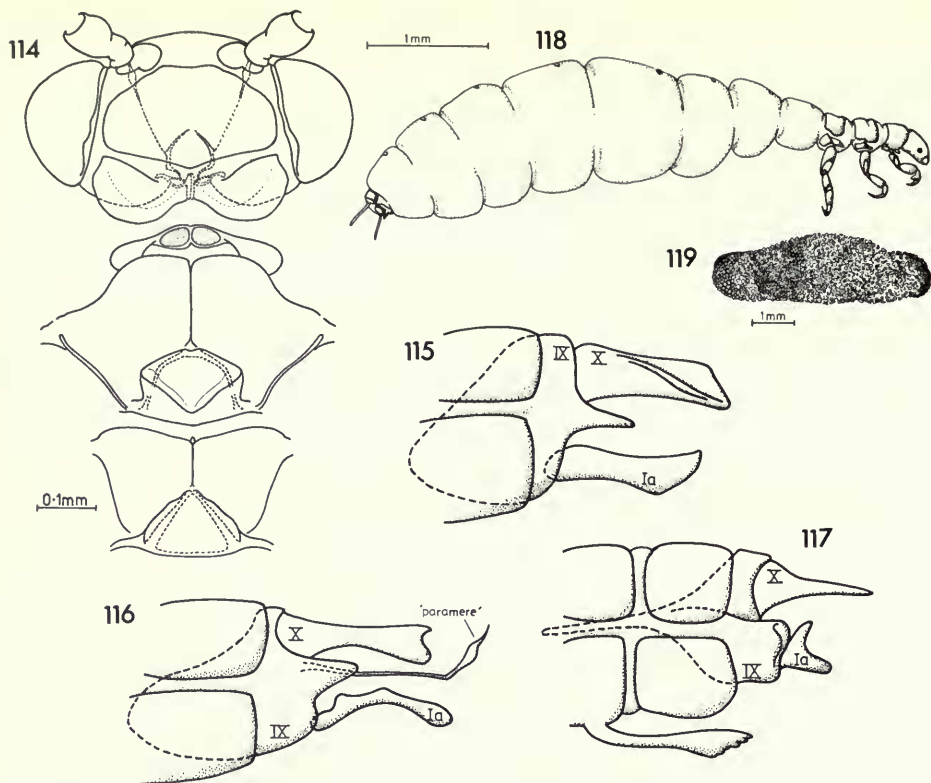
The *uncinata*-group: a small Palaearctic group with characteristic male genitalia which have an affinity with those of the *sparsa*-group.

The *capensis*-group: a small African group possibly derived from the *sparsa*-group.

The *consimilis*-group: a large Nearctic group with a distinctive basic male genitalia form which is close to that of the Palaearctic *sparsa*-group.

The *occulta*-group: a distinct group of approximately 25 species with a distribution extending throughout Europe into Asia Minor, Africa and SE. Asia and with at least 4 Nearctic representatives; male genitalia (Fig. 116).

The *tineoides*-group: *tineoides* is the only Palaearctic member of this predominantly Nearctic group (*moselyi* Ulmer from Peking may also belong here); male genitalia (Fig. 117).



Figs 114–119 *Hydroptila*. 114, adult head and thorax, dorsal view (♂). 115–117, generalized ♂ genitalia; (115) *sparsa*-group; (116) *occulta*-group; (117) *tineoides*-group (vide Figs 15, 16). 118, larva, lateral view; 119, case, lateral view.

The *dikirilagoda*-group: a distinct group of three species from Sri Lanka; possibly related to the *tineoides*-group.

The *losida*-group: a small group of Australasian species (Australia, Tasmania, Solomon Islands (Guadalcanal), New Guinea) which may have some affinity with the SE. Asian members of the *occulta*-group such as *panchaoi*.

The *pulchricornis*-group: a small group of Palaearctic species with possibly one N. African representative.

The *forcipata*-group: of three Palaearctic species; Schmid (1959b) considers that *armathai* belongs here but this is dubious.

The *vectis*-group: two Palaearctic species.

The *tigurina*-group: three distinctive European species with very characteristic sidepieces to segment IX of the male genitalia.

The *waubesiana*-group: a very distinct Nearctic group of seven species.

Incertae sedis: a number of species have not been assigned to any group owing to the unavailability of material for study and the inadequacy of descriptions in the literature.

GENERIC SYNONYMS. *Oxydroptila* is a small genus of only two species, *furcata* Martynov from India and *kirilawela* Schmid from Sri Lanka, which is distinguished from *Hydroptila* on minor venational differences and the form of the male genitalia which is said to resemble that of *Oxyethira*, especially with respect to segment VIII. As in *Hydroptila*, ocelli are absent and the spur formula is 0.2.4; examination of a male paratype of *kirilawela* (BMNH) has revealed the presence of postoccipital scent organs and a thoracic structure identical to that of *Hydroptila*. Contrary to Martynov (1935) and Schmid (1958a), the male genitalia do not resemble those of *Oxyethira* and

the female genitalia of *kirilawela*, as figured by Schmid (1958a), form a simple oviscapt and not the modified, specialized condition characteristic of *Oxyethira* (q.v.). The larvae are unknown. It is therefore proposed to sink *Oxydroptila* as a junior synonym of *Hydroptila* and, although both *furcata* and *kirilawela* are included in the incertae sedis group, they probably form a distinct species unit.

Oeceotrichia, *Pasiotrichia* and *Sumatranotrichia* are three monotypic genera described by Ulmer (1951) from Indonesia (the Sunda Islands) and distinguished from *Hydroptila* solely on minor venational differences. Each has a spur formula of 0.2.4, ocelli absent, male genitalia of the *Hydroptila* pattern and, from examination of type-material (UHZIM loan), postoccipital scent-organs (males) and a thorax identical with those of *Hydroptila*. According to the descriptions and figures of the larvae and cases given by Ulmer (1957), these are also almost identical with those of *Hydroptila* (notably with respect to the fore-tibial process and the three caudal filaments). It would thus appear that *Oeceotrichia*, *Pasiotrichia* and *Sumatranotrichia* are all junior synonyms of *Hydroptila*, the constituent species showing certain affinities, according to the forms of the male genitalia, to the SE. Asian members of the *occulta*-group (e.g. *panchaoi* Schmid) and the Australasian *losida*-group.

As an additional point it was noted, during the examination of Ulmer's Sunda Island material that two females in spirit labelled *Pasiotrichia* bore no resemblance to *Hydroptila*: sp. A had no ocelli but had a thorax resembling that of *Orthotrichia*, and sp. B had 3 ocelli and a thorax similar to that of *Oxyethira* or *Tricholeiochiton*. However, I was not able to identify the specimens positively owing to their fragile conditions.

The following records of material found in the BMNH collections may also be of interest (all det. J. E. Marshall): *palestinae* Botosaneanu & Gasith (1 ♀, Southern Yemen 'W. Aden Protectorate', 1937, Scott & Britton); *triloba* Kimmins (1 ♂, Solomon Islands, Guadalcanal, J. D. Bradley); *vectis* Curtis (1 ♂, Spain, Prov. Granada, Valley of Guadelfeo, 3.vii.1969, Sattler & Carter).

Genus *OXYETHIRA* Eaton

Oxyethira Eaton, 1873 : 143. Type-species: *Hydroptila costalis* Curtis sensu Eaton, by original designation. *Lagenopsyche* Müller, 1879a : 39. Type-species: *Lagenopsyche spirogyrae* Müller, by subsequent designation by Fischer, 1961. [Synonymized by Fischer, 1961.]

Argyrobothrus Barnard, 1934 : 392. Type-species: *Argyrobothrus velocipes* Barnard, by monotypy. [Synonymized by Ross, 1948.]

Loxotrichia Mosely, 1937 : 165. Type-species: *Loxotrichia azteca* Mosely, by original designation. [Synonymized by Ross, 1944.]

Dampftrichia Mosely, 1937 : 169. Type-species: *Dampftrichia ulmeri* Mosely, by original designation and monotypy. [Synonymized by Ross, 1944.]

Oxytrichia Mosely, 1939a : 289. Type-species: *Oxytrichia mirabilis* Mosely, by original designation and monotypy. [Synonymized by Kimmins, 1966.]

DISTRIBUTION. Cosmopolitan (excluding polar regions).

Oxyethira is a very successful genus of approximately 75 species with a world-wide distribution and with very distinctive larvae which feed on green filamentous algae. The true identity of the type-species is still in dispute. Eaton originally proposed the genus for two species, *Hydroptila costalis* Curtis and *H. albiceps* McLachlan, the latter being an endemic New Zealand species. Eaton (1873) considered *costalis* (Curtis) to be a senior synonym of *H. tineoides* Dalman sensu Stephens and, doubtfully, of *H. flavicornis* Pictet. However, subsequent dissection of Curtis's male type of *costalis* by Neboiss (1963) showed this to be conspecific with *Orthotrichia tetensii* Kolbe, the latter being placed as a junior synonym of *costalis* (Curtis) and congeneric with *angustella* (McLachlan), the type-species of *Orthotrichia*. The next available name for *costalis* (Curtis) sensu Eaton is *Oxyethira flavicornis* (Pictet).

This is still not an unequivocal solution to the problem, however, since Pictet's type-specimen of *flavicornis* has not yet been located (one female specimen in Geneva is labelled 'Zurich 9/81' and a second specimen has no abdomen according to Neboiss, 1963). Neboiss therefore merely proposes the synonymy as 'one of the possible answers' but does not ignore the fact that *flavicornis*

Pictet could be a synonym of *H. tineoides* Dalman sensu Stephens, thus leaving *costalis* (Curtis) sensu Eaton without a name. However, until the problem can be resolved (and this is unlikely since Pictet's type appears to be missing), the proposal of Neboiss (1963) must be accepted. Nevertheless, there is no doubt as to the actual species referred to by Eaton since his figures of the distinctive male genitalia are clearly recognizable (he merely considered that *costalis* Curtis was the same species).

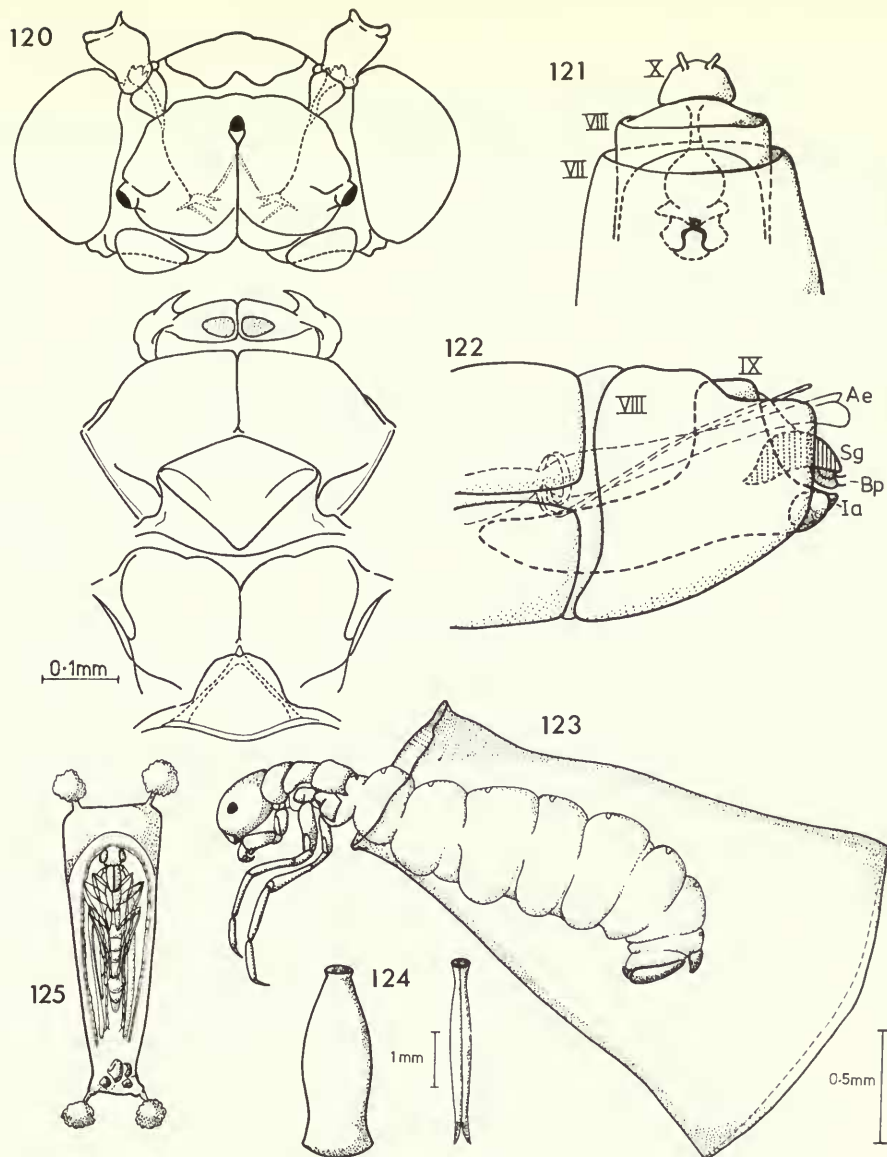
The larval stages of *Oxyethira* (discounting Pictet's (1834) figures of *H. flavicornis*) were first described by Müller (1879a) as *Lagenopsyche spirogyrae* Müller from Brazilian material. The first description of British material was by Morton (1887) from specimens of *O. costalis* (Curtis) sensu Eaton sent to him by McLachlan and Hudson (1886) described larvae of an unidentified New Zealand hydroptilid which subsequently proved to be *O. albiceps* McLachlan. The most detailed larval description is that of *O. costalis* (Curtis) sensu Eaton as given by Nielsen (1948) upon which the generic diagnosis given below is partly based. The following list summarizes the published descriptions of species of *Oxyethira* larvae to date (the type-species will now be called *flavicornis*).

O. albiceps (Mosely & Kimmins, 1953); *delcourtii* (Jacquemart, 1973); *distinctella* (Lepneva, 1964); *dualis* (Sibley, 1926); *ecornuta* (Lepneva, 1964); *flavicornis* (Nielsen, 1948; Lepneva, 1964; Hickin, 1967); *frici* (Lepneva, 1964); *hyalina* (Müller, 1879a); *incana* (Ulmer, 1957); *meridionalis* (= *unidentata*) (Jacquemart & Coineau, 1962); *puertoricensis* (Flint, 1964); *sagittifera* (Lepneva, 1964); *serrata* (Ross, 1944); *simplex* (Macdonald, 1950; Hickin, 1967); *tristella* (Lepneva, 1964); *velocipes* (Barnard, 1934).

Apart from Kimmins's (1958) paper on the British species of *Oxyethira* there has been no previous review of the genus as a whole. The following diagnosis and species-groupings have been based on published species descriptions and examination of adult and larval material in the BMNH collections. To date there are approximately 75 species which fall into more or less distinct species-groups each distinguished by the form of the male genitalia. The status of *Stenoxethira* Kimmins will be discussed later but, according to Schmid (1958a), it should be considered a synonym of *Oxyethira*.

DIAGNOSIS. *Adult.* Forewing length 2.5–3.5 mm: head and antennae unmodified (Fig. 120); anterior tentorial arms reduced medially; ocelli 3; thorax (Fig. 120) – mesoscutellum with anterior margin convex and posterior margins slightly concave, metascutellum convexly subtriangular: spur formula 0.3.4: ♀ genitalia a modified oviscap (Fig. 121) (after Kimmins, 1958) with sternite VI with a short, acute ventral process; segment VII with tergite and sternite more or less fused, ventral apical margin sometimes excised; tergite VIII reduced to a narrow arched band, the centre of its apical margin produced as a spatulate lobe; sternite VIII forming a short 'subgenital plate'; tergite IX either free or fused to VIII, short and hood-like; tergite X forming a short, broad plate carrying two short slender cerci; details of internal vaginal structures obscure but apparently with an upper and lower lobe, the latter with a conspicuous baso-ventral process directed caudad: ♂ genitalia (Fig. 122) (after Kimmins, 1958) with sternite VII with short, acute ventral process; segment VIII with tergite and sternite more or less fused, apical margins dorsally and ventrally excised, that of tergite with dorsal or lateral processes, the latter sometimes armed with stout spines; segment IX mostly withdrawn into VIII, its upper half generally much shorter than lower, often reduced to a short transverse band, lateral apical margins of IX sometimes produced or with variously formed spiniform processes, ventral margin generally excised and from which arises a lobe; tergite X obscure, membranous; subgenital appendages represented by two sclerotized plates attached to segment IX, fused basally with their apices variously hooked downwards ('fused claspers' (Kimmins, 1958); 'lower penis cover' (Mosely, 1939a); 'subgenital plate' (Ross, 1948)); above and arising from them are two pairs of short, membranous 'bilobed' processes each terminating in a short apical seta; aedeagus long and slender with a spiniform 'titillator' arising at midlength.

Larva (Fig. 123). Head elongate, of uniform diameter, slightly laterally compressed; dorsal and ventral ecdysial lines distinct; postnotal sclerites paired, anterior ventral apotome well developed, U-shaped with a distinct transverse ridge, posterior ventral apotome present (Fig. 27); labrum with strongly convex lateral margins and deep median anterior indentation; mandibles asymmetrical – left with projecting blades bearing small teeth and with a median brush, right with blades poorly defined and distal only, teeth only near apices; thoracic pleurites of each segment fused except for the free anal epimeron of the prothorax; three sternites present on each thoracic segment (Fig. 41); forelegs short with small baso-ventral setate lobe on femur and long distal process bearing a ventral row of short, spine-like setae on tibia



Figs 120–125 *Oxyethira*. 120, adult head and thorax, dorsal view; 121, generalized ♀ genitalia, ventral view; 122, generalized ♂ genitalia, lateral view (*vide* Figs 15, 16); 123, early fifth instar larva in case, lateral view; 124, late fifth instar larval case, lateral views; 125, pupa in case, ventral view.

(chelate); mid- and hindlegs twice as long as forelegs, tarsal claws long and slender: abdomen typically distended, intersegmental constrictions distinct; laterally compressed and usually held in characteristic comma-shaped attitude; dorsal 'rings' present on segments II–VII; tergites absent except on segment IX; anal prolegs fused to side of segment X; caudal gills absent.

The early instars of *flavicornis* (Pictet), as *costalis* (Curtis), are described and figured in Nielsen (1948).

Case (Figs 123, 124). Laterally compressed, semi-transparent, constructed of secretion only; 'jug-' or 'bottle'-shaped; posterior end broad with slit-like opening, anterior end narrow, constricted to form a neck with a well-defined rim around the opening. The pupal case (Fig. 125) is basically a sealed larval case attached horizontally to the substrate by four short ligaments, each with an adhesive disc and arising from each corner (in some species there are two ligaments from each of the anterior corners); the pupa

lies with its head towards the broad (hence anterior) end (cf. larva), with its dorsum towards the substrate; the case is closed anteriorly by a narrow curved membrane, the posterior neck being filled with a plug of silk; the pupal cases usually occur on aquatic plants, rarely on submerged rocks or wood.

Pupa. Typically hydroptilid; mandibles long with serrate inner blades.

BIOLOGY. The larvae are generally considered to occur in plant thickets in slow-moving and static bodies of water in association with the green filamentous algae upon which they feed. This is true for *distinctella*, *ecornuta* and *sagittifera*, for example (Lepneva, 1964), and also *velocipes* (Barnard, 1934) and *spirogyrae* (Müller, 1879c) but a number of species are reputed to frequent faster-flowing streams where the larvae are found on the rocky substrate in areas covered with algae; these are *frici* and *tristella* (Lepneva, 1964), *azteca* (or *janella*) (Flint, 1968a) and *hyalina* (Müller, 1879c). *O. flavicornis* (Pictet) (*costalis* Curtis sensu Eaton) is a pond dweller although, in Pictet's (1834) original description, the larva of *flavicornis* is reputed to occur in fast-flowing streams with *Hydroptila pulchricornis* Pictet, thus casting further doubts on the identity of *flavicornis* (see above). In Illinois, Ross (1944) records pupae of *serrata* from the underside of rocks in about 1 m of water along the open beaches of glacial lakes. Pupal cases of *albiceps* in New Zealand, according to Hudson (1886), were found attached to stones in streams, especially in the late summer when 'the rivers are generally very low . . . and a luxurious growth of green slime weed is present'. Finally, *puertoricensis* is found in all types of streams and at all elevations in Jamaica (Flint, 1968b) and, on Puerto Rico (Flint, 1964), the cases are found 'in tangles of filamentous green algae' and are fixed to irregularities in the rocks at pupation.

The larvae are highly specialized for feeding on filamentous algae and for living in masses of vegetation as indicated by their chelate forelegs, laterally compressed bodies and very long, slender mid- and hindlegs. According to Siltala (1907) gut contents of an *Oxyethira* species included diatoms and entire algal filaments and Jacquemart & Coineau (1962) similarly record diatoms and desmids (the normal food source is reputed to be simply the fluid contents of algal cells). Nielsen (1948) describes the case building behaviour of *flavicornis* while Jacquemart & Coineau (1962) describe the similar habits of an unidentified *Oxyethira* species.

SPECIES-GROUPS. At least 10 species-groups may be recognized by the form of the male genitalia. The following groupings have been based on relationships suggested in original species descriptions and have been verified by me as far as the literature and available material would allow. The lists of species are given in the checklist.

The *falcata*-group: essentially a western Palaearctic group of seven species, three occurring only in the Atlantic Islands, and with possibly one Nearctic representative. Two species (*falcata* and *frici*) are British. The group is distinguished by the spinose postero-lateral processes of the male segment VIII. There is still some doubt as to the status of *fischeri* and *dentata* which both have very similar genitalia to those of *falcata*; as Higler (1974) points out in his paper on *fischeri*, *falcata* may exhibit 'eco-geographic' forms (after Jacquemart & Coineau, 1962) and he considers that *dentata* may belong to one of these forms. However, Higler believes that *fischeri* is distinct from *falcata*, mainly on account of features of the male aedeagus (based on the figures of *falcata* in Jacquemart & Coineau, 1962) although Mosely's (1939a) figures of the aedeagus of *falcata* are very similar to Higler's figures of *fischeri*! A thorough study of *falcata* and its reputed close relatives is obviously required in order to sort out this species-complex. *O. borella* also is close to *falcata* but would seem to be distinct according to both male and female genitalic characters (Svensson & Tjeder, 1975).

The *flavicornis*-group: a Palaearctic group extending from Europe (and Egypt) to Korea with perhaps one species from Sri Lanka. It may be related to the Nearctic *rivicola*-group and is distinguished by the absence of a median ventral lobe on the fused claspers and the broad, widely separated subgenital plates (in ventral view).

The *rivicola*-group: possibly related to the *flavicornis*-group and, although essentially Nearctic, may contain a number of Neotropical members (from Surinam, described by Flint, 1974).

The *simplex*-group: again possibly related to the *flavicornis*-group; this group may require further investigation as, at present, it contains two geographically distinct elements: *simplex* and

tristella from northern Europe and NW. U.S.S.R., and *paramartha*, *ramosa*, *harpagella* and *galekoluma* (and, possibly, *Stenoxyethira excisa*) from SE. Asia.

The *distinctella*-group: a small Holarctic group distinguished by the prominent dorso-lateral posterior serrate processes of the male segment VIII.

The *azteca*-group (= *Loxotrichia* Mosely): a small group from Central America and the Antilles, characterized by the form of the male segment IX. *O. archaica* Malicky from Portugal would also appear to belong here, its occurrence in this region possibly being a result of a chance introduction from S. America (the group occurs, for example in Brazil); it is unlikely that it is an early Tertiary relict as stated by Malicky (1975).

The *ulmeri*-group (= *Dampftrichia* Mosely): another small Nearctic group distinguished by the dorso-lateral tapering processes of segment IX.

The *zeronia*-group: essentially Central American and characterized by the anterior prolongation of the ventral margin of segment IX.

The *pallida*-group: a small but distinct Nearctic group of uncertain affinities.

The *bidentata*-group: a Nearctic–Neotropical group of three species.

The *mirabilis*-group: containing *mirabilis* (Palearctic) and *flagellata* (Reunion Island); the latter has some affinity with *bidentata* which itself was once included with *mirabilis* in the genus *Oxytrichia*.

Incertae sedis: of these, *albiceps* is endemic to New Zealand and *velocipes* to South Africa; *spirogyrae* and *hyalina* (*Lagenopsyche*) from Brazil are known only in their larval stages; *incana* (Indonesia) was described from the female and larva only (Ulmer, 1951; 1957), while *angustella* is known from the wings alone. *O. anabola* and *berneri* are distinct Nearctic species while *mithi*, from Greece, has not yet been placed.

Genus *STENOXYETHIRA* Kimmins

Stenoxyethira Kimmins, 1951 : 207. Type-species: *Stenoxyethira minima* Kimmins, by original designation.

Gnathotrichia Ulmer, 1951 : 59. Type-species: *Gnathotrichia isabellina* Ulmer, by original designation and monotypy. **Syn. n.**

DISTRIBUTION. SE. Asia (Burma, Indonesia).

Kimmins (1951) erected *Stenoxyethira* principally for the type-species, *minima*, but included, somewhat doubtfully, *excisa* Kimmins on the basis of the general similarity of the wing venation. The genus is here considered to contain just these two species with *Gnathotrichia isabellina* treated as a synonym of *Stenoxyethira excisa*. The following generic diagnosis is based on Kimmins (1951). The immature stages are unknown.

DIAGNOSIS. *Adult.* Forewing length 1.6 mm: head and antennae unmodified; ocelli 3; spur formula 0.2.4 (0.3.4 in *excisa* and *isabellina*): ♂ genitalia (cf. Fig. 122) with segment VIII forming a ring concealing segment IX, latter narrow and lightly sclerotized dorsally, ventral margin produced as a rounded, bilobed plate (fused inferior appendages ?) above which is a triangular, trough-shaped subgenital plate; tergite X difficult to interpret; aedeagus rod-like, with a single spine or sheath.

S. excisa was included in this genus on the basis of venational features, being distinguished from *minima* by the presence of a small spine or microscopic spur on the mid-tibia, the form of the aedeagus and the produced spines of segment VIII of the male genitalia. Kimmins (1951) was in no way satisfied with this arrangement and noted on the card for *Stenoxyethira* in the BMNH index (Hydroptilidae) ‘? = *Gnathotrichia* Ulmer, 1951’. I noted independently of Kimmins the similarity between these two genera when examining type-material of *G. isabellina* Ulmer (UHZIM loan) and concluded that this species, from Java and Sumatra, was probably synonymous with *S. excisa* Kimmins. According to the dates of publication (Kimmins, March, 1951; Ulmer, April, 1951) *S. excisa* takes priority. However, as Schmid (1958a) points out, *S. excisa* may truly belong in *Oxyethira*, being closely related by the form of the male genitalia and wing venation to *O. galekoluma* Schmid from Sri Lanka (the venation of the latter approaching that of *G. isabellina* and *O. angustella* Martynov). I agree that there is a similarity in form which is also supported by the spur formula (0.3.4) and the structure of the thoracic nota, but I do not agree with Schmid

that Kimmins's figures of the male genitalia of *S. excisa* are inverted in comparison with those of *O. galekoluma* (Schmid, 1958); on the contrary, it is Schmid who has misinterpreted their orientation.

It would thus seem that *Stenoxyethira* and *Gnathotrichia* should be regarded as synonyms of *Oxyethira*, at least with regard to *S. excisa*. The status of *S. minima* is not so easily resolved – as regards venational and male genitalic characters it could well be a specialized member of *Oxyethira*, although it is the only species so far recorded without a preapical spur on the mid-tibia. This may simply prove to be a specific or even individual variation; as in most of these problems the solution must await the collection and examination of further material. In conclusion, therefore, it is proposed to retain the genus *Stenoxyethira* for the time being with *Gnathotrichia* as a junior synonym although the latter should probably more correctly be placed as a synonym of *Oxyethira* along with *Stenoxyethira excisa*. In this case the genus *Stenoxyethira* may need to be retained solely for the type-species, *minima*, although this may also prove to belong in *Oxyethira*.

Genus *PAROXYETHIRA* Mosely

Paroxyethira Mosely, 1924 : 670. Type-species: *Paroxyethira hendersoni* Mosely, by subsequent designation by Mosely & Kimmins, 1953.

DISTRIBUTION. New Zealand.

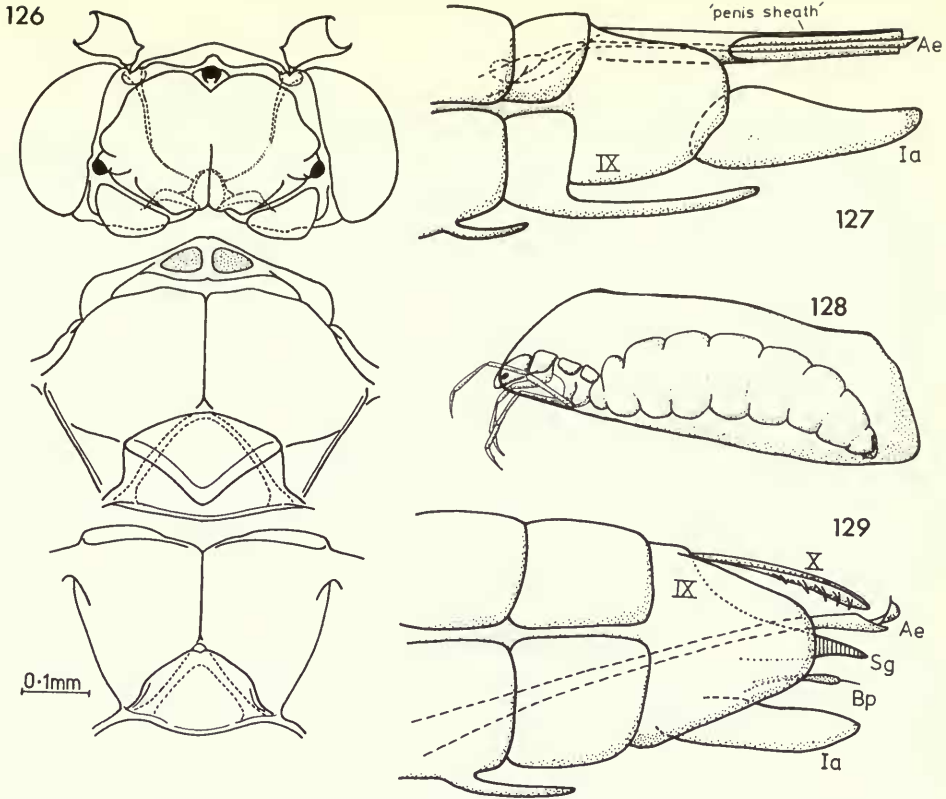
This endemic New Zealand genus contains five species although I believe that further species are at present being described (F. B. Michaelis, pers. comm.). Mosely (1924) originally described *eatoni*, *tillyardi* and *hendersoni*; *hintoni* and *kimminsi* being subsequently described by Leader (1972) in which paper a key to all males and females was provided. Leader (1970) also discussed the function of the setal equipment of the early and fifth instar larvae of *Paroxyethira*, giving very generalized figures of each but no detailed morphological descriptions. *Paroxyethira* is characterized by the unique forms of both the male and female genitalia, especially the elongate inferior appendages and ventral processes of the former, and the general appearance of the larva and its case. The following diagnosis is based on Leader (1972) and Mosely's original material (BMNH collection).

DIAGNOSIS. *Adult*. Forewing length 2.5–3.5 mm: anterior tentorial arms reduced to fine strands medially (Fig. 126); antennae of approximately 25–40 segments; ocelli 3: thorax (Fig. 126) as in *Xuthotrichia*: spur formula 0.3.4: ♀ genitalia a modified oviscapt with sternite VI with a small ventral 'tooth'; posterior margin of sternite VII with a triangular ventral process; tergite VIII deeply excised dorsally and elongate postero-ventrally, almost meeting mid-ventrally; sternite VIII small, appearing as a small lobe just above the projection from VII; segment IX small, mostly concealed by VIII; segment X small, bilobed, each lobe with a short apical cercus: ♂ genitalia (Fig. 127) with sternite VII with an elongate flattened ventral process extending beyond the posterior margin of segment IX; segment IX fused, with a deep postero-dorsal excision such that the segment is incomplete dorsally; tergite X absent; inferior appendages basically elongate, concave with apices directed inwards; aedeagus with a very characteristic basal, sleeve-like sheath with the posterior margin produced as a long spine extending almost to the apex of the aedeagus, latter long and slender with a short, broad proximal region which tapers anteriorly to a distinct constriction just before which arises a spiral process or 'titillator'.

Larva (Fig. 128). According to Leader (1972) the larva of *Paroxyethira* differs from that of *Oxyethira* only in the possession of a complex spine on the ventral process of the fore-tarsus which resembles the fan-like seta present on the fore-tarsus of *Hydroptila* (cf. Fig. 47). As in *Oxyethira*, the legs of *Paroxyethira* are longer and more slender than those of *Hydroptila* but apart from these general points no further comparisons can be drawn. Leader (1972) states that the five species of *Paroxyethira* can only be distinguished by the fine sculpturing of the thoracic sternites which, however, tends to be rather an inconsistent feature and thus not a reliable taxonomic character.

Case (Fig. 128). 'Purse-type', constructed of secretion only, oblong and sometimes with outward pointing anterior and posterior ventral spines as extensions of the ventral seam by which the case is attached to the substrate (pupal).

BIOLOGY. According to Pendergrast & Cowley (1966), the larvae of *hendersoni* are abundant in vegetation in lakes, ponds and streams where filamentous green algae occur. Leader (1972) briefly gives collecting data for each species.



Figs 126–129 Hydroptilini, *Oxyethira*-group. 126–128, *Paroxyethira*; (126) adult head and thorax, dorsal view; (127) generalized ♂ genitalia, lateral view; (128) larva in case, lateral view. 129, *Xuthotrichia*, generalized ♂ genitalia, lateral view (vide Figs 15, 16).

DISCUSSION. From features of the adult head and thorax and the basic form of the female genitalia, I consider *Paroxyethira* to be closely allied to the endemic Australian genus *Xuthotrichia* Mosely. The general morphology and habits of the larvae suggest that it may, along with *Xuthotrichia*, be an offshoot of the *Oxyethira* branch of the Hydroptilini.

Genus *XUTHOTRICHIA* Mosely

Xuthotrichia Mosely, 1934 : 139. Type-species: *Xuthotrichia ochracea* Mosely, by original designation.

DISTRIBUTION. Australia.

This endemic Australian genus is known from the four original species described by Mosely (1934) (*ochracea*, *simplex*, *fimbriata* and *eskensis*), and I believe that more species are being described (A. Wells, *in litt.*) and there are specimens of an unidentified (and possibly new) species from Western Australia in the BMNH collections.

The genus is characterized by the unique form of the male genitalia which show considerable specific variation; they are asymmetrical and often very complex, and identification of species is very difficult from Mosely's original descriptions. The females have not been described but from examples in the unidentified material in the BMNH collections mentioned above the genitalia appear to bear some resemblance to those of *Paroxyethira*. The immature stages are unknown although a figure of an unidentified Australian hydroptilid larva in Riek (1970) greatly resembles that of *Paroxyethira* in general appearance (cf. Fig. 128) and, if so, may be the larva of *Xuthotrichia* (see *Paroxyethira* account). The case of the larva figured in Riek (1970) is constructed of silk and sand-grains although, according to A. Wells (*in litt.*), the cases of larvae which she believes

to be of *Xuthotrichia* (larvae not described, however) are of secretion only but of a slightly different shape to those of *Paroxyethira* (also of secretion only). It would be necessary to compare specimens of the two genera, however, before any conclusions regarding affinities could be drawn.

The following diagnosis is based on a study of material in the BMNH collections (Mosely's types) and the original descriptions.

DIAGNOSIS. *Adult.* Forewing length 2.5–3.0 mm: anterior tentorial arms reduced to fine strands medially; antennae c. 40-segmented; ocelli 3: mesoscutellum similar to that of *Hydroptila* and *Oxyethira* (cf. Figs 114, 120); metascutellum pentagonal with slightly anteriorly convergent lateral sides: spur formula 0.3.4: ♂ genitalia (Fig. 129) – sternite VII with a moderately long, slender ventral process; segment VIII unmodified; segment IX fused, usually obliquely truncate in lateral view, dorsal and ventral margins more or less excised; tergite X, inferior appendages, subgenital appendages, subgenital plate and bilobed process very variable; aedeagus long and slender, without a median constriction or spiral process but sometimes with additional short lateral processes arising just before apex.

BIOLOGY. According to A. Wells (*in litt.*), the larvae of *Xuthotrichia* occur in all types of still water in Australia such as lakes, billabongs, etc.

DISCUSSION. *Xuthotrichia* may be closely related to *Paroxyethira* as indicated by adult head and thoracic features (and also, possibly, by the general form of the larva); these genera may in turn be allied to the cosmopolitan genus *Oxyethira*.

Genus *TRICHOLEIOCHITON* Kloet & Hincks

Leiochiton Guinard, 1879 : 139. Type-species: *Leiochiton fagesii* Guinard, by monotypy. [Preoccupied by *Leiochiton* Curtis, 1831 in Coleoptera.]

Tricholeiochiton Kloet & Hincks, 1944 : 97. [Replacement name for *Leiochiton* Guinard.]

Synagotrichia Ulmer, 1951 : 81. Type-species: *Synagotrichia fortensis* Ulmer, by original designation and monotypy. **Syn. n.**

DISTRIBUTION. W. Palearctic; SE. Asia (Burma, Indonesia).

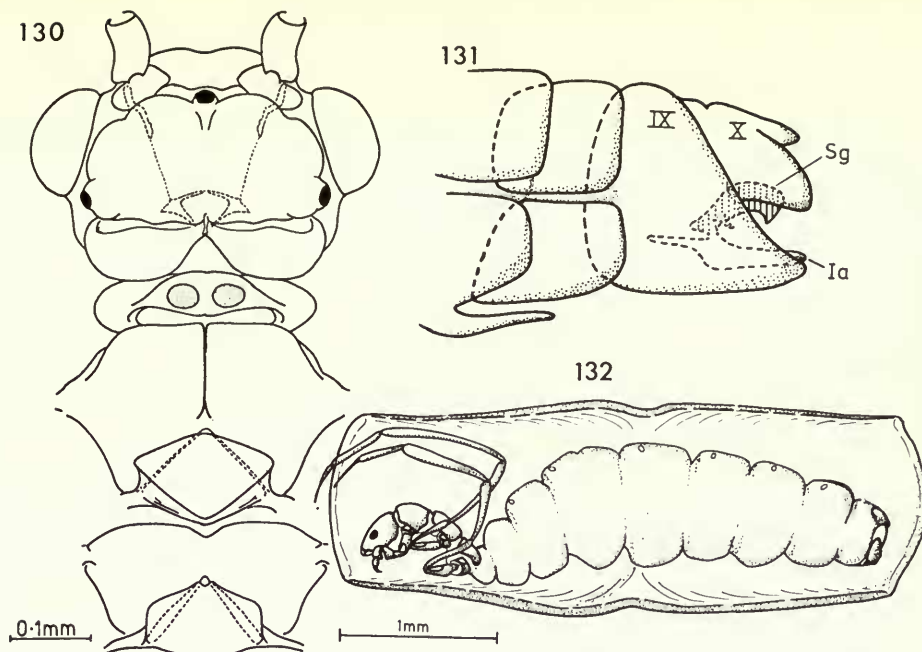
The genus *Tricholeiochiton* contained originally only two species, *fagesii* (Guinard), which is known locally from Europe and the U.S.S.R., and *lacustris* Kimmins from Burma (S. Shan States). Examination of type-material of *Synagotrichia fortensis* Ulmer (UHZIM loan) reveals that this genus should be regarded as a junior synonym of *Tricholeiochiton*.

The unique larva of *fagesii* was first noticed by Bremi who gave an extended description of it under the name of *Hydroptila flabellifera* in a letter to Hagen which was published by the latter in 1864. Hagen considered the species to belong to the genus *Agraylea* due, possibly, to the shape of the case which was covered with filaments of 'Confervae' (?). However, it is now known that the cases of *Tricholeiochiton* are constructed of secretion only and that Bremi's *H. flabellifera* consisted of a mixed series of *T. fagesii* and *Agraylea sexmaculata* Curtis.

The next reference to the larva was in 1867 when Dr Barker presented a series to the Dublin Microscopical Society as specimens of Diptera. Then, in 1878, Guinard published figures of the larva and, albeit rather crudely, the male genitalia, and named the species *Leiochiton fagesii*. The species has since been variously referred to as *Oxyethira fagesii* and *O. felina* Ris, and was first recorded on the British list by Mosely (1932) who subsequently recognized the synonymy with *L. fagesii* (Mosely, 1939a). The generic name was changed to *Tricholeiochiton* by Kloet & Hincks (1944) when it was discovered that *Leiochiton* was preoccupied in Coleoptera.

The larva of *fagesii* has been described a number of times but not in any great detail. The account given below is based on Lepneva (1964) and a study of material donated to the BMNH by Dr B. Higler (Netherlands) and Dr I. D. Wallace (MCM). A formal description has not been given since it is understood that Wallace (pers. comm.) proposes to publish a full account based on recently discovered British material.

Kimmins (1951) described a second species, *lacustris*, from Burma in which the male genitalia are almost identical with those of *fagesii* except for the presence of a long ventral process on the seventh abdominal sternite. The immature stages of *lacustris* are unknown.



Figs 130–132 *Tricholeiochiton*. 130, adult head and thorax, dorsal view; 131, generalized ♂ genitalia, lateral view; 132, larva in case, lateral view.

From the form of the male genitalia, wing venation and shape of the metascutellum, *Synagotrichia fortensis* Ulmer, from Indonesia (Sumatra), probably represents a third species of *Tricholeiochiton*. Discovery of the larval stages, however, would confirm this view.

DIAGNOSIS. *Adult*. Forewing length 2.25–3.00 mm: anterior tentorial arms reduced to fine strands medially (Fig. 130); antennae of c. 37 segments in *lacustris*; ocelli 3: metascutellum pentagonal, lateral sides slightly divergent anteriorly: spur formula 0.3.4: lateral processes of abdominal sternite V absent, basal pit with characteristic sculpturing in *fagesii* (Fig. 13): ♀ genitalia an oviscapt: ♂ genitalia very distinct, but very similar in the three known species (Fig. 131) – sternite VII sometimes with a long, slender ventral process; segment VIII unmodified; segment IX fused, produced ventro-posteriorly (obliquely truncate in lateral view), dorsal and ventral posterior margins deeply incised; segment X forming a dorsal membranous lobe with a pair of postero-ventrally produced lateral processes which partly enclose the aedeagus; inferior appendages small, fused baso-medially, contained within ventral incision of IX and concealed by latero-ventral processes of IX; subgenital plate transverse with down-curved posterior ‘lip’ and produced antero-ventrally to join the inferior appendages, base of plate with a pair of small seta-bearing processes, junction of plate and inferior appendage produced anteriorly as a slender truncate process; aedeagus short and robust with a distinct median constriction, just before which arises a slender spiral ‘titillator’ which has a slightly dilated apex (homologies of genitalia uncertain).

Larva (Fig. 132). Head long and slender with parallel sides; dorsal ecdysial lines indistinct anteriorly; tentorial pits distinct; ‘postmental sclerites’ crescent-shaped, undivided, with short blunt postero-median process (Fig. 23); mandibles typically subtriangular with slender pointed apices, left with bluntly toothed dorsal blade: thoracic nota paired; three well-developed sternites on prothorax only (Fig. 46); pleurites with preepisternite fused in all three segments (according to Lepneva, 1964); forelegs short, tibiae with distinct disto-ventral processes bearing apical spines and a row of short ventral setae; mid- and hindlegs characteristically very long and slender, achieved by elongation of trochanter, femur, tibia and tarsal claw: abdomen long, more slender than in other Hydroptilidae, characteristically curved; tergite on segment IX only; anal prolegs fused to X, anal claw short; dorsal ‘rings’ present on segments III–VIII.

Case (Fig. 132). ‘Purse-type’, oblong, ‘sac-shaped’, sides slightly convex, constructed of secretion only.

Pupa. Undescribed but pupal case with two stalked attachment discs at each anterior corner and one at each posterior corner.

BIOLOGY. According to Lepneva (1964) the larvae of *fagesii* inhabit stagnant and slow-moving bodies of water in plant thickets, the pupal cases being attached to the undersides of aquatic plants.

DISCUSSION. The form of the male aedeagus and the algae-associated habits of the larval stages indicate that *Tricholeiochiton* is a member of the Hydroptilini. Although obviously very specialized with respect to both the male genitalia and the morphology and habits of the larvae, the general appearance of the latter and the form of the adult head and thorax are suggestive of the genus *Oxyethira*, of which branch of the Hydroptilini *Tricholeiochiton* may be an early offshoot. The disjunctive distribution of this genus is rather unusual with only two Oriental and one Palaearctic representatives. The latter may have been due to an early introduction of ancestral stock from the Oriental region.

Tribe **ORTHOTRICHINI** Nielsen *stat. n.*

Orthotrichiinae Nielsen, 1948 : 186. Type-genus: *Orthotrichia* Eaton, 1873.

Nielsen erected the subfamily Orthotrichiinae for two genera, *Orthotrichia* and *Ithytrichia*, on the basis of larval morphological and behavioural affinities. Although the adults and larvae are very distinctive for each genus, the larvae exhibit a number of fundamental similarities which distinguish them from other members of the Hydroptilinae. However, according to certain adult features, such as the structure of the head and thorax and the male aedeagus, the Orthotrichiini appears to have arisen from an early Hydroptilini-type ancestor. I therefore propose to accept Nielsen's original grouping but as a tribe of the subfamily Hydroptilinae and with the inclusion of *Ithytrichia* remaining open to further speculation; the latter may later be found to form a distinct unit on its own.

DIAGNOSIS. *Adult.* Forewing length 2–4 mm; tentorium complete (Figs 133, 139); ocelli 3 or 0; post-occipital lobes unmodified; thoracic nota variable (Figs 133, 139); mesonotum without transverse suture: spur formula 0.3.4; abdominal sternite V with typical setate process: ♀ genitalia basically a simple oviscapt, modified in *Orthotrichia* (Fig. 134): ♂ genitalia very characteristic for each genus, highly asymmetrical in *Orthotrichia* (Figs 135, 140); aedeagus with spiral 'titillator'.

Larva. Both *Orthotrichia* and *Ithytrichia* have very distinct and specialized larval stages. Their characteristic features, on the basis of which Nielsen (1948) grouped the genera together, are as follows. Labium broad and flat; mandibles flattened, tapering; general form of the ventral apotome and 'postmental sclerites' (Figs 24, 28); the thoracic sternites (Fig. 42); the comb-like setae of the fore-coxae; the circle of 'rings' on abdominal segment I and the single median caudal filament from segment X. The cases of the larvae of each genus are also very characteristic, neither being of the typical 'purse-type'.

Pupa. Typically hydroptilid, mandibles long and untoothed.

DISCUSSION. According to Nielsen (1948) *Ithytrichia* and *Orthotrichia* may be derived from a common ancestor which was probably associated with filamentous green algae; this, in my opinion, probably occurred early in the evolution of the Hydroptilini. *Orthotrichia* became a highly efficient algal feeder living in plant thickets in sluggish to still water while *Ithytrichia*, possibly in association with the colonization of rheophilous and semi-exposed habitats, secondarily adopted the detritus-feeding habit but retained a number of morphological features derivable from algal-feeding ancestors. Such features which are shared by *Ithytrichia* and *Orthotrichia* larvae are the broad, flat labium; the flattened mandibles; the form of the ventral apotomes and postmental sclerites (cf. Figs 24, 28) and the thoracic sternites (Fig. 42); the comb-like setae of the fore-coxae; the complete circle of abdominal 'rings' on segment I and the possession of a single median caudal filament which, according to Nielsen (1948), is present in the early instars of *Orthotrichia*.

On the basis of these larval affinities, Nielsen proposed the subfamily Orthotrichiinae for *Orthotrichia* and *Ithytrichia* and, although the larvae and adults of these two genera have evolved along different lines, I am retaining Nielsen's grouping but as a tribe of the Hydroptilinae. The Orthotrichiini is thus, on the basis of the form of the adult thorax, male aedeagus and fundamental larval associations with filamentous algae, a highly specialized and probably early offshoot of the Hydroptilini line. *Orthotrichia* is a very successful genus which has a wide present-day distribution

although no species have yet been recorded from the Neotropical and Australian regions. *Ithytrichia* is less well represented with only three recognized Holarctic species and possibly one Indonesian. Until the genus is better known, however, its origins and evolutionary history must remain speculative.

Genus *ORTHOTRICHIA* Eaton

Orthotrichia Eaton, 1873 : 141. Type-species: *Hydroptila angustella* McLachlan, by original designation. *Clymene* Chambers, 1873 : 114. Type-species: *Clymene aegerfasciella* Chambers, by monotypy. [Synonymized by Flint, 1966.]

Javanotrichia Ulmer, 1951 : 75. Type-species: *Javanotrichia maeandrica* Ulmer, by original designation. **Syn. n.**

Orthotrichiella Ulmer, 1951 : 79. Type-species: *Orthotrichiella ranauana* Ulmer, by original designation and monotypy. **Syn. n.**

Baliotrichia Ulmer, 1951 : 88. Type-species: *Baliotrichia litoralis* Ulmer, by original designation and monotypy. **Syn. n.**

DISTRIBUTION. Holarctic; Africa; SE. Asia (to New Guinea).

Orthotrichia is a very successful genus with approximately 40 species and with an almost continuous world-wide distribution, although it has not so far been recorded from Central or South America or the Australian region. The genus is well represented in the Palaeotropical regions of Africa and SE. Asia, through Indonesia (Sunda Islands) to New Guinea (Papua) and, possibly, Fiji and Borneo (unidentified species, BMNH collections, det. J. E. Marshall). The adults are characterized by the uniquely developed asymmetrical male genitalia and the absence of ocelli (cf. *Hydroptila* which may be distinguished by the presence of postoccipital scent organs in the males). The larvae are associated with aquatic vegetation in standing waters and are highly specialized for feeding on the cell contents of green filamentous algae.

The genus was erected by Eaton (1873) for *angustella* (McLachlan) and *atra* (Hagen), the latter being transferred to *Stactobia* by McLachlan (1884). *O. tetensii* Kolbe was subsequently found by Neboiss (1963) to be a junior synonym of *Hydroptila costalis* Curtis (vide *Oxyethira*) and Flint (1966) showed *Clymene aegerfasciella* to be a senior synonym of *Orthotrichia americana* Banks.

The larva of *costalis* was described in detail by Nielsen and that of *angustella* by Jacquemart (1962b), although no distinguishing features were indicated in the latter work for separating the two species. It should be noted that Jacquemart's figure of the dorsal view of the head of *angustella* does not make it clear that the anterior beak is an extension of the labrum; it has also been drawn pointing in the opposite direction to that as figured by Nielsen.

Regarding the genera described by Ulmer (1951) from the Sunda Islands, larvae are described by Ulmer (1957) for *Orthotrichiella ranauana* and *Baliotrichia litoralis*. The relationships of these two genera, as well as that of *Javanotrichia*, with *Orthotrichia* are discussed below.

The following generic diagnosis is based on the literature and examination of adult and larval material in the BMNH collections.

DIAGNOSIS. *Adult.* Forewing length 2–4 mm; wings markedly attenuate, forewings with a row of black, flattened basal subcostal setae in males of the *angustella*-group: tentorium (Fig. 133) complete; antennae of 30–40 segments; postoccipital lobes prominent, subspherical, but not modified as scent-organs; ocelli 0: thorax (Fig. 133) – metascutellum characteristically rectangular: spur formula 0.3.4: ♀ genitalia a modified oviscapt (Fig. 134), segment VIII fused and sclerotized, segments IX and X membranous, IX short: ♂ genitalia (Fig. 135) characteristically asymmetrical; sternites VI and VII variously with ventral processes or tufts of setae; segment VIII unmodified; segment IX fused, often with asymmetrical, posterolateral processes; inferior appendages usually small and fused medially, but well developed, porrect and strongly curved in *costalis*; subgenital appendages indistinct or absent; bilobed process present (*Bp*); tergite X forming a large, asymmetrical dorsal plate, ventrally concave, often with laterally directed dorsal spines; beneath X is a variously shaped, slender, asymmetrical sclerite usually with two asymmetrical processes, one of which is long and slender and lies diagonally beneath X and alongside the aedeagus (according to Nielsen, 1970, a similar structure was described by Ulmer, 1951, for *Javanotrichia*, *Orthotrichiella* and *Sumatranotrichia*); aedeagus very long and slender with distinct proximal and distal halves near the junction of which arises a slender, spiral 'titillator'.

Larva (Fig. 136). Slightly depressed dorso-ventrally: dorsal ecdysial lines of head distinct; postmental sclerites and anterior ventral apotomes as in Fig. 28; labrum asymmetrical with a beak-like median process (Fig. 137); mandibles slender, flat, asymmetrical (Fig. 32); thoracic nota paired; mid- and hind-legs just slightly longer than forelegs; fore-tibia without a ventral process or modified setae; each tarsus with a distal, flattened, plate-like spur; fore-coxa with comb-like rows of setae; preepisternite of prothorax free; paired anal sternites present on all three thoracic venters, fused in prothorax (Fig. 42); abdomen cylindrical, slightly broader at midlength; segment II with a pair of lateral 'humps'; dorsal 'rings' present on segments III–VIII, segment I with a complete circle of 'rings' near anterior margin; tergite present on segment IX only; median caudal filament in early instars only.

Case (Fig. 138). Of the 'wheat-seed' type, almost circular in cross-section, tapering gradually towards slit-like anterior and posterior openings; convex dorsal surface characteristically ribbed, ventral surface flat.

Pupa. Typically hydroptilid but mandibles short; pupal case attached by a single attachment disc at each end.

BIOLOGY. The larvae prefer slowly running and sometimes almost stagnant water in plant thickets. According to Nielsen (1948) the larva bites into each cell of a filament of green algae and enlarges the hole by inserting the labral beak; the cell contents are then sucked out. This is a more efficient mechanism than that found in *Agraylea*, *Hydroptila* and *Oxyethira*. In addition there have been two reports (Burton & McRae, 1972; Disney, 1973) of *Orthotrichia* larvae feeding on *Simulium* (Diptera) larvae, but it was not evident as to whether these were cases of active predation or of the hydroptilids mistaking the *Simulium* for algal filaments.

SPECIES-GROUPS (see checklist). The 36 species may be split into four main groups on the basis of the form of the male genitalia.

The *angustella*-group: exclusively 'Old World' with the majority of representatives being recorded from the regions of Africa and SE. Asia (the latter region may include the species originally described by Ulmer, 1951, in *Javanotrichia*, *Baliotrichia* and *Orthotrichiella* from Indonesia, see group 2); *angustella* is the only truly Palaearctic representative and has a very wide distribution extending from northern Europe (including the British Isles) to northern Africa and from Iberia to the Urals; the group is characterized by the development of the lateral processes of segment IX in the males and the row of subcostal scales on the forewings of the males of most species.

The *litoralis*-group: the species mentioned above from Indonesia originally described by Ulmer (1951; 1957) as *Javanotrichia*, *Baliotrichia* and *Orthotrichiella* may form a distinct group; it also includes species described by Schmid (1958a) from Sri Lanka.

The *costalis*-group: a small 'Old World' group; *costalis* is the most common species and has a wide European distribution (including the British Isles) and has also been recorded from the Sudan, U.S.S.R. and Japan; the group is distinguished by the absence of lateral processes on segment IX and the small, more or less symmetrical inferior appendages in the males.

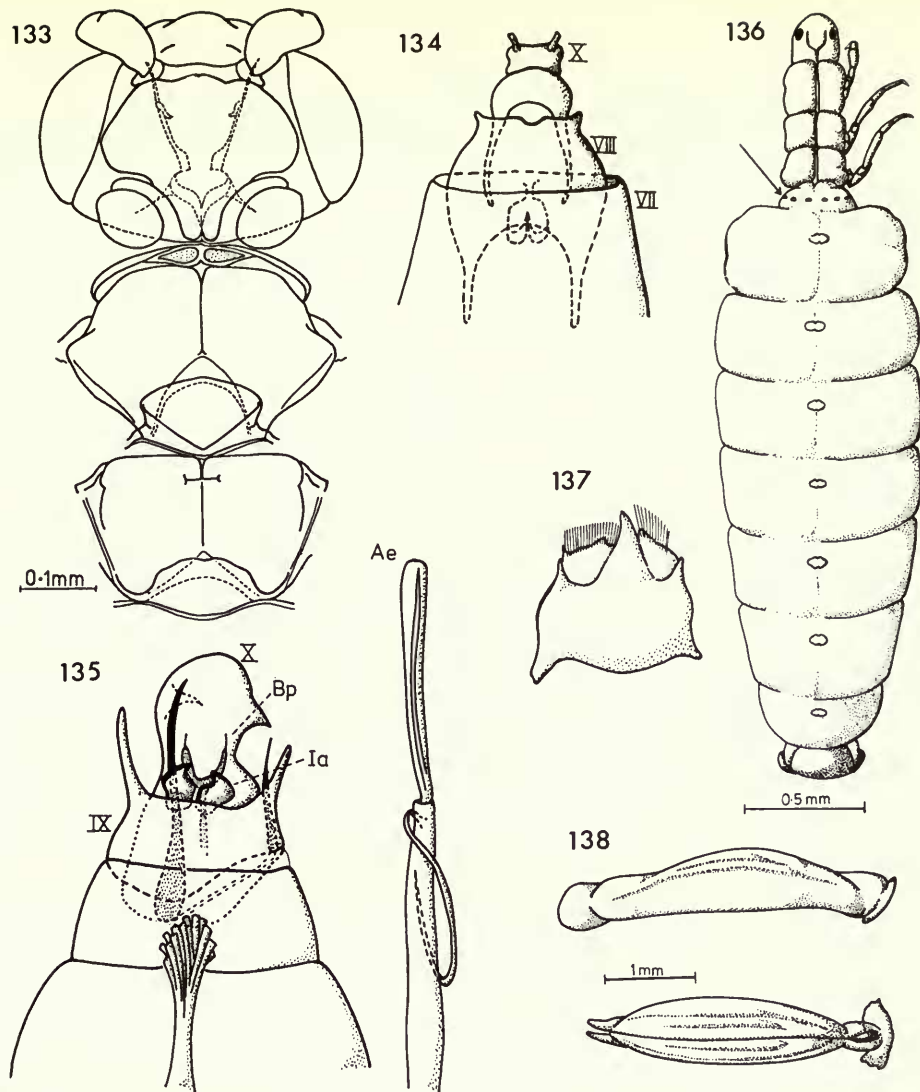
The *aegerfasciella*-group: principally Nearctic in distribution with one well-established Palaearctic representative (*tragetti*); the group is characterized by the lateral development of the asymmetrical inferior appendages of the males.

A fifth group may also be recognized.

The *kokodana*-group: this consists of two distinct species from Papua New Guinea characterized by the simplicity of the male genitalia. (N.B. there are unassociated ♀ specimens of *Orthotrichia* spp. from Fiji and Borneo in the BMNH collections.)

GENERIC SYNONYMS. The genera discussed below are here considered to be junior synonyms of *Orthotrichia*.

Javanotrichia Ulmer contains three species, *maeandrica* Ulmer and *curvata* Ulmer from Indonesia and *dampfi* Ulmer from Egypt. Ulmer (1951) distinguished the genus from *Orthotrichia* solely on venational characters but, as can be seen from other adult features such as the absence of ocelli, spur formula 0.3.4 and the distinctive asymmetrical form of the male genitalia in *Javanotrichia*, these two genera are probably synonymous. Examination of type-material (UHZIM loan) reveals that the structure of the thorax of *J. curvata* is typical of *Orthotrichia*; in addition the male genitalia are very similar to those of *O. avicularis* Kimmins from India. *J. dampfi* greatly



Figs 133–138 *Orthotrichia*. 133, adult head and thorax, dorsal view; 134, generalized ♀ genitalia, ventral view; 135, generalized ♂ genitalia, ventral view and aedeagus (vide Figs 15, 16); 136, larva, dorsal view; 137, larval labrum, dorsal view; 138, pupal case, lateral and dorsal views.

resembles other African *Orthotrichia* species, such as *O. benguelensis*, especially with respect to the spinose lateral processes of segment IX in the male. The immature stages are unknown.

Baliotrichia Ulmer contains *litoralis* Ulmer from Indonesia (Bali) and four species from Sri Lanka (Schmid, 1958a). As in *Javanotrichia* the genus is only distinguished on minor venational features. According to Schmid (1958a) the male genitalia of *B. udawarama* bear a 'curious similarity' to those of *O. extensa* Martynov from India while, in my opinion, the genitalia of *B. litoralis* are most like those of *O. avicularis* Kimmins. The larva and case of *B. litoralis*, as described by Ulmer (1957), are unmistakably those of *Orthotrichia* and thus, taking both adult and larval features into account, I propose that *Baliotrichia* be placed as a synonym of *Orthotrichia*.

Orthotrichiella Ulmer is a monotypic genus from Indonesia again only distinguished from *Orthotrichia* on minor venational features. Examination of type-material (UHZIM loan) indicates

that the two genera are synonymous and this is supported by the appearance of the immature stages described by Ulmer (1957).

In conclusion these three small tropical genera provide a natural geographical link with the *Orthotrichia* species from the mainland and New Guinea, this genus being previously unrecorded from the Indonesian region.

DISCUSSION. The genus *Orthotrichia* is a specialized and very successful recent member of the Hydroptilinae with a wide continuous present-day distribution. It is the only hydroptilid genus which has a truly tropical component (cf. the Stactobiini which, although tropical, are confined to the relict cool montane areas of SE. Asia and Africa) and probably owes its success to its tolerance of still water conditions and its specialized, efficient larval feeding habits.

Genus *ITHYTRICHIA* Eaton

Ithytrichia Eaton, 1873 : 139. Type-species: *Ithytrichia lamellaris* Eaton, by original designation and monotypy.

Saranganotrichia Ulmer, 1951 : 83. Type-species: *Saranganotrichia decussata* Ulmer, by original designation and monotypy. **Syn. n.**

DISTRIBUTION. Holarctic.

Ithytrichia is a small genus at present containing only four species. *I. lamellaris* is the most common Palaearctic species while *clavata* Morton, originally described from North America, was found by Tjeder (1930) to occur in Sweden and has since been recorded from France, Great Britain and Finland (Karelia) and may prove to be the only hydroptilid with a truly Holarctic distribution (cf. *Agraylea multipunctata* which may involve a species complex). *I. mazon* Ross from Illinois is known only from the holotype male while *bosniaca* Botosaneanu, a Yugoslavian species described from the immature stages only, is regarded as a doubtful species by Botosaneanu (1967).

The larva of *lamellaris* has been described several times, the most detailed account being given by Nielsen (1948). That of *clavata* has not positively been identified although the larva referred to by Needham (1902) and figured by Ross (1944), as well as that described by Wiggins (1977), is probably this species.

Saranganotrichia decussata Ulmer from Indonesia (Java) is known from both the adult and larval stages (Ulmer, 1951 and 1957 respectively) of which the latter show distinct affinities with *Ithytrichia* in the form of the case, larval head shape and possession of abdominal 'buds'. However, the male genitalia of *Saranganotrichia* are atypical of *Ithytrichia* and thus cast doubts on the associations of the adults and larvae. Examination of Ulmer's specimen of *decussata* (adult) failed to reveal any diagnostic characters as the microscopical preparation was in a very poor condition. Nevertheless, on the basis of the affinities of the larval stages, it is proposed here that *Saranganotrichia* be placed as a synonym of *Ithytrichia* until the true identity of the adults is discovered.

The following generic diagnosis is based on the literature and on examination of material in the BMNH collections.

DIAGNOSIS. *Adult.* Forewing length 3 mm: tentorium complete (Fig. 139); antennae with 20–25 segments; ocelli 3: thorax (Fig. 139) with mesoscutellum with anterior margin convex, posterior edge separated from posterior margin of mesonotum by a narrow strip; metascutellum with a strongly convex anterior margin: spur formula 0.3.4: abdominal sternite V with typical setate processes, although shorter than usual and in a faintly sculptured pit (Fig. 14): ♀ genitalia an oviscap, segment VIII with median ventral sclerite: ♂ genitalia distinct (Fig. 140); sternite VI sometimes with a short ventral spine; segments VI and VII unmodified; IX and X membranous dorsally, former incomplete ventrally but with lateral sides tapering posteriorly ('side-pieces' (Tjeder, 1930)) and with a hook-like structure arising ventrally near the apex; in *lamellaris* tergite X bears two characteristic parallel rod-like sclerites; inferior appendages slender, arising from antero-ventral margin of segment IX and extending to its lateral apex; subgenital plate with short postero-medial processes bearing short setae and attached basally to the apical hooks of IX; aedeagus long, well developed, with distinct proximal and distal halves divided by a median constriction by which arises the spiral 'titillator'.

Larva (Fig. 141). Head broad with slight median lateral bulges in region of 'eyes', flattened, tapering anteriorly both dorso-ventrally and laterally: dorsal ecdysial lines distinct; postmental sclerite hemispherical, ventral apotome V-shaped, prominent (Fig. 24); labrum long and narrow, curved sides tapering anteriorly, anterior margin of sclerite with three shallow indentations, narrow anterior membranous portion with straight anterior margin; mandibles very flat (even more so than in *Orthotrichia*, cf. Fig. 32), left with short lower blade, serrated upper blade and median brush, apices of both mandibles pointed with a small basal tooth on upper blade; pleurites of prothorax only with three distinct sclerites; prothoracic venter with unpaired anal sclerite (as in *Orthotrichia*) with lateral ends fused with posterior corners of nota (Fig. 42); median oral sternites present on meso- and metathoracic venters only: legs short, subequal, forelegs without trochanteral, femoral or tibial processes; fore-coxae with comb-like rows of setae: abdomen greatly compressed laterally, segment I very small, II with large lateral processes, III–VI with characteristic dorsal and ventral 'bud-like' processes, VII with dorsal process only, VIII with postero-ventral projection; segment I with complete circle of dorsal 'rings'; IX with tergite which projects 'roof-like' above anal prolegs (fused to X) and covering the base of the single median caudal filament.

Case (Fig. 142). This consists of secretion only and resembles a pumpkin seed; narrow anteriorly with an oval ridged opening flanked by the lateral valves, 'slit' only open medially. The thorax of the larva may be extended through the narrow anterior opening and, due to the ability of the thorax and first abdominal segment to rotate on the rest of the abdomen, the case is usually carried horizontally (cf. the lateral compression of the abdomen). Consequently, the ventral surface of the case is slightly more convex while the anterior ventral margin is slightly indented so that the hindlegs may be held free of the case.

Pupa. Typical; mandibles long, without teeth. The pupal case is sealed and held, with the ventral side towards the substrate, by a single median posterior filament with a broad attachment disc, and an anterior cylindrical plug which also broadens into a single attachment disc.

BIOLOGY. According to Lepneva (1964) the larvae of *lamellaris* prefer running water, brooks and rivulets in plant thickets while Nielsen (1948) records them as being distinctly rheophilous, occurring in the strong current on exposed parts of submerged vegetation and smooth, current-swept stones, the cases being held flat against the substrate. I. D. Wallace (pers. comm.) has collected *Ithytrichia* larvae (probably *lamellaris*) from amongst willow roots in fine silt along with larvae of an *Orthotrichia* species. According to Ulmer (1957) the larvae and pupae of *S. decussata* occur in flowing water amongst moss and leaves, in waterfalls, spring-channels and mountain brooks.

Although Nielsen (1948) did not observe the feeding behaviour of *lamellaris* larvae, he considers them to be detritus-feeders unlike the specialized algal-feeding larvae of *Orthotrichia* to which *Ithytrichia* is supposed to be allied. The flattened labial lobe may be adapted to serve as a shovel for scooping up diatoms and other detritus from the substrate, the food then being conveyed to a groove on the ventral surface of the labrum along which it passes to the pharynx. Nielsen considers the anterior tapering of the head to be associated with such feeding habits while the flattened pointed mandibles, although apparently not adapted for scraping or scooping, may be derived from the *Orthotrichia*-like condition (cf. Fig. 32), their function being taken over by the labium.

INCERTAE SEDIS

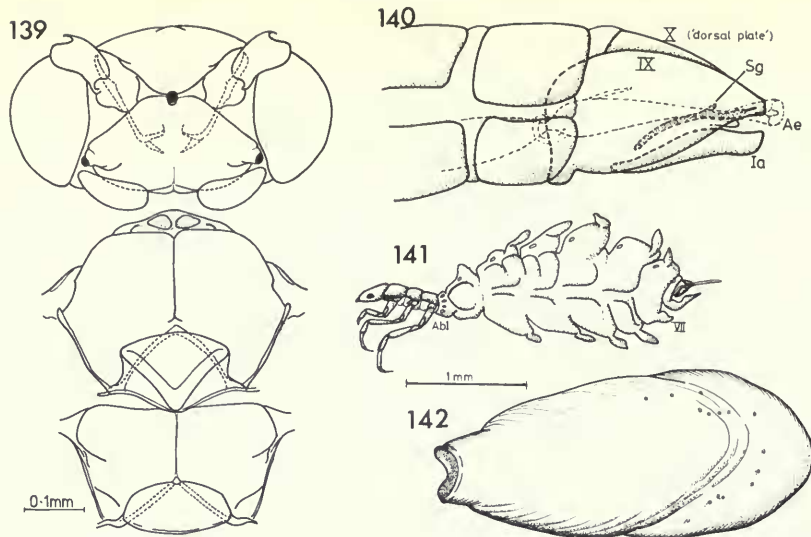
The following group of essentially monotypic and geographically distinct genera have not been assigned to any particular tribe due to the inadequacy of the existing data, the insufficiency or unavailability of well-preserved material or, as in the case of *Caledonotrichia* and *Dibusa*, the unique morphological features which cannot be likened to those of any other hydroptilid genus. All would, however, appear to be members of the subfamily Hydroptilinae; *Caledonotrichia* and *Dibusa* have typically hydroptilid larvae while all have hydroptilid adult features except *Dicaminus* which is known from the larval cases only. *Electrotrichia* is only known from Baltic Amber and appears to be a distinct but now extinct genus.

Genus *MACROSTACTOBIA* Schmid

Macrostactobia Schmid, 1958a : 46. Type-species: *Macrostactobia elawalikanda* Schmid, by original designation and monotypy.

DISTRIBUTION. Sri Lanka.

This monotypic genus is known only from the original series from Sri Lanka, of which there



Figs 139–142 *Ithytrichia*. 139, adult head and thorax, dorsal view; 140, generalized ♂ genitalia, lateral view (vide Figs 15, 16); 141, larva, lateral view; 142, larval case, lateral view.

is a single paratype male in the BMNH collections. The adult diagnosis given below is based on Schmid (1958a), the main characteristic being the unique form of the male genitalia. The larvae are unknown.

DIAGNOSIS. *Adult.* Forewing length 2.5–3.0 mm; head without large postoccipital lobes; antennae 18-segmented; ocelli 3; mesoscutellum subtriangular (BMNH specimen): ♂ genitalia with sternites VII and VIII very narrow; sternite IX enlarged ventrally but not invaginated into the preceding segments; segment X of two distinct halves; inferior appendages complex and fused along their midlength; aedeagus a long narrow tube.

BIOLOGY. The species is reported to inhabit 'rivers at moderate altitudes'.

DISCUSSION. Schmid places *Macrostactobia* at the base of the *Macrostactobia*–*Parastactobia*–*Plethus*–*Chrysotrichia* branch (of the Stactobiini), its primitiveness being indicated by its more complete wing venation and its relatively larger size. The genitalia are stated to exhibit the typical (stactobiine) characters of the group, the line of evolution resembling that of *Parastactobia* as suggested by the great development of segment IX at the expense of those preceding, and the long and rigid appendages.

The male genitalia are unique but while the antennae are of 18 segments only, as is typical of the Stactobiini, the metathorax does not have the rectangular form characteristic of this tribe. Consequently I can give no positive indications as to the true affinities of this very specialized monotypic genus but can merely stress the need for the examination of additional material.

Genus *DIBUSA* Ross

Dibusa Ross, 1939 : 66. Type-species: *Dibusa angata* Ross, by original designation and monotypy.

DISTRIBUTION. U.S.A. (N. Carolina, Tennessee, Arkansas, Kentucky, Oklahoma).

This North American genus is known only from the type-species. Ross (1939) first described the male and the larva has since been described by Wiggins (1977). The form of the male genitalia is unique within the Hydropitilidae but the associated larvae show unequivocally that *Dibusa* is a true member of the family. The following generic diagnosis is based on Ross (1939; 1944) and Wiggins (1977) and examination of larvae (USNM loan).

DIAGNOSIS. *Adult.* Forewing length 5.5 mm; head and antennae unmodified; ocelli 0; wing venation relatively complete, wings elliptical, ovate; spur formula 1.3.4: ♂ genitalia with segment IX retracted into

eighth, with sclerotized sides and a membranous dorsum; tergite X fused with IX, divided into a pair of lateral sclerotized plates separated on the meson by membranous folds and curved downward at the apex to form a short hook; the 'cerci' arise as a small lobe in the middle of the lateral margin at the base of tergite X; inferior appendages biramous, ventral lobe slightly enlarged and upturned at apex, dorsal lobe more slender, out-curved and widest at middle; aedeagus with a filiform basal portion, markedly enlarged near base, and a semimembranous irregularly tapering pointed apex.

Larva (Figs 143, 144), after Wiggins (1977). Head suboval in lateral view (i.e. not compressed): distinctly paired thoracic nota on all segments; pleurites fused on all thoracic segments; legs short, subequal, robust; tarsal claws unique being stout and strongly curved with a thick, blunt spur basally on each (but smaller than that of *Stactobiella*, cf. Figs 144 and 80); abdomen moderately distended, not markedly depressed or compressed, intersegmental grooves distinct; abdominal tergites present only on segment IX; dorsal 'rings' present on segments I–VIII; anal prolegs fused to segment X.

Case (Fig. 145). Typically 'purse-like', of two adpressed silken valves covered with pieces of the red freshwater alga *Lemanea*.

BIOLOGY. The larvae collected by Neff and Resh (Wiggins, 1977) were associated with the red freshwater alga *Lemanea*, the pupal cases being attached to the base of the algal thallus.

DISCUSSION. The relationships of *Dibusa* are not clear because no material was available for an examination of the diagnostic features of the adult head and thorax. However, from the general features of the adults, larvae and cases, *Dibusa* would appear to be a very specialized early offshoot of the tribe Hydroptilini. The relatively complete adult wing venation and the generalized form of the larva with its 'purse-type' case are very primitive features whereas the absence of ocelli, the unique male genitalia and the larval associations with *Lemanea* (and not the usual, more common green filamentous algae as in the Hydroptilini) indicate specialization. The more primitive features are suggestive of affinities with *Agraylea* (Hydroptilini) and *Nothotrichia* (*incertae sedis*) (vide Flint, 1967b).

Genus *NOTHOTRICHIA* Flint

Nothotrichia Flint, 1967b : 56. Type-species: *Nothotrichia illiesi* Flint, by original designation and monotypy.

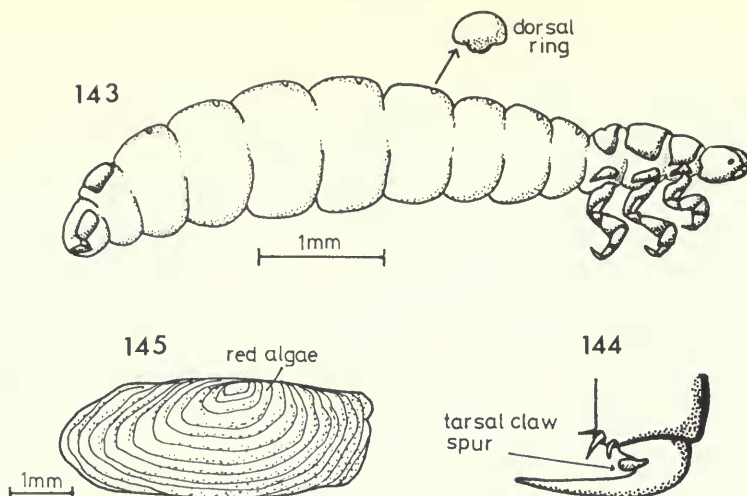
DISTRIBUTION. South America (Chile).

This monotypic genus has so far been recorded only from Chile, the type being collected in the Cautin Province in 1957 by Professor J. Illies with further specimens being taken by Flint and Cekalovic in 1966.

Flint (1967b) provides the basis of the generic diagnosis given below which is supplemented by observations on the head and thoracic structure as seen in a female specimen of *illiesi* (USNM loan). The larval stages are unknown.

DIAGNOSIS. *Adult.* Forewing length 3.5 mm: head and antennae unmodified; ocelli 3; wings not markedly narrowed but with pointed apices; venation relatively complete; spur formula 1.3.4: thorax (Fig. 146); mesoscutellum without transverse suture, anterior margin strongly convex; metascutellum deep, subquadrate, but with strongly convex anterior angles: ♂ genitalia (after Flint, 1967b) with segment IX incomplete dorsally, with a broad flap from dorsal angles; tergite X membranous, posterior margin trilobate; inferior appendages broad, large, 'mitten-like', with a small baso-dorsal 'thumb'; aedeagus with slightly expanded apex and apico-lateral process arising at midlength and contiguous with the central aedeagal duct, non-spiral 'titillator' present.

DISCUSSION. This unique endemic Chilean genus may represent a descendant of an early offshoot of the Hydroptilini branch which evolved in isolation in this part of the Neotropical region. This is indicated by the relatively complete venation, presence of 3 ocelli, presence of a fore-tibial spur, an undivided mesoscutellum and the non-spiral 'titillator' of the aedeagus. The male genitalia appear to be derived from the basic hydroptilid form but are specialized in that they are greatly simplified. Discovery of further species and the immature stages may give some insight into the true relationships of this genus.



Figs 143–145 *Dibusa angata* Ross. 143, larva, lateral view; 144, larval tarsus, lateral view; 145, larval case, lateral view.

Genus *DICAMINUS* Müller

Dicaminus Müller, 1879a : 39. Type-species: *Diaulus ladislavii* Müller, by subsequent monotypy.

Diaulus Müller, 1879c : 142. Type-species: *Diaulus ladislavii* Müller, by monotypy. [Synonymized by Fischer, 1961.]

DISTRIBUTION. South America (Brazil).

Müller (1879a) described a number of caddis cases from Brazil amongst which were some very distinct forms which had two dorsal 'chimneys' and were covered in diatoms. Müller considered these to belong to hydroptilid larvae and described them under the generic name of *Dicaminus* (Latin: of two chimneys), although neither a description of the larva nor a species name were given. In subsequent papers Müller (1879c; 1880) refers to these cases as being of the hydroptilid *Diaulus ladislavii*, thus naming the species and giving *Diaulus* (the Greek equivalent of *Dicaminus*) as the generic name. As stated by Fischer (1961), *Dicaminus* takes priority over *Diaulus* and consequently receives its type-species.

The following description of the cases is from Müller (1879c).

DESCRIPTION. The strongly laterally compressed oval cases have slit-like anterior and posterior openings and are covered in diatoms. On the dorsal margin they bear two (rarely three) cylindrical chimneys which facilitate the passage of water through the case without, according to Müller, the incessant exertions of the larva as seen in other hydroptilids where the case simply has slits at either end. The pupal cases are fixed vertically along their whole ventral margin to the upper side of stones 'and often these little houses form large villages of a rather picturesque aspect'. The larval case is reported to be 2.5 mm long by 0.75 mm broad.

DISCUSSION. The relationships and validity of this genus are not known since only the cases of the immature stages have been described. Müller's original material, which has not yet been traced, may contain larvae and pharate adults which will permit a more positive identification.

Genus *ORPHNINOTRICHIA* Mosely

Orphnino-trichia Mosely, 1934 : 138. Type-species: *Orphnino-trichia maculata* Mosely, by original designation and monotypy.

DISTRIBUTION. Australia (New South Wales).

The holotype of this endemic Australian genus is the only known specimen and it is in such a

poor condition (BMNH collection, slide mount) that details of the genitalia and thorax cannot be interpreted clearly.

Mosely erected the genus on the basis of the unique wing venation while the male genitalia also appear to be unlike those of any other hydroptilid genus. Since the thoracic structure, female genitalia and larval stages are unknown, the genus cannot be placed with any certainty at present. However, from the simplicity of the male genitalia and the form of the aedeagus, with its distinctive spiral 'titillator', the genus may have affinities with the Hydroptilini, differing from *Hydroptila* in the possession of ocelli, the absence of cephalic scent-organs and venation, and from *Oxyethira* in venation and spur formula.

DIAGNOSIS. *Adult.* Forewing length 2.75 mm: tentorium incomplete; antennae 32-segmented; ocelli 3: spur formula 0.2.4: ♂ genitalia with sternite VII bearing a short spinous process; segment VIII unmodified; segment IX fused, deeply excised dorsally, appearing bifurcate from above and containing the membranous tergite X which tapers posteriorly to a pointed apex; subgenital plate not distinguishable unless it is fused with or replaces the 'inferior appendages'; 'inferior appendages short but slender, fused along almost entire mid-line except for a short distance apically (this structure may represent the subgenital plate, the inferior appendages being absent or vestigial as the two small medio-ventral processes of segment IX); aedeagus with a broad proximal region separated from the longer more slender distal region by a median constriction just anterior to which arises the spiral process or 'titillator'.

Genus *CALEDONOTRICHIA* Sykora

Caledonotrichia Sykora, 1967 : 585. Type-species: *Caledonotrichia illiesi* Sykora, by original designation.

DISTRIBUTION. New Caledonia.

This small endemic New Caledonian genus contains two species, *illiesi* and *minor*, both described by Sykora (1967) from material collected in 1966 by Professor J. Illies. I have been able to examine adult, larval and pupal material of unidentified and undescribed species of *Caledonotrichia* kindly loaned to me by Professor H. H. Ross of Athens, Georgia.

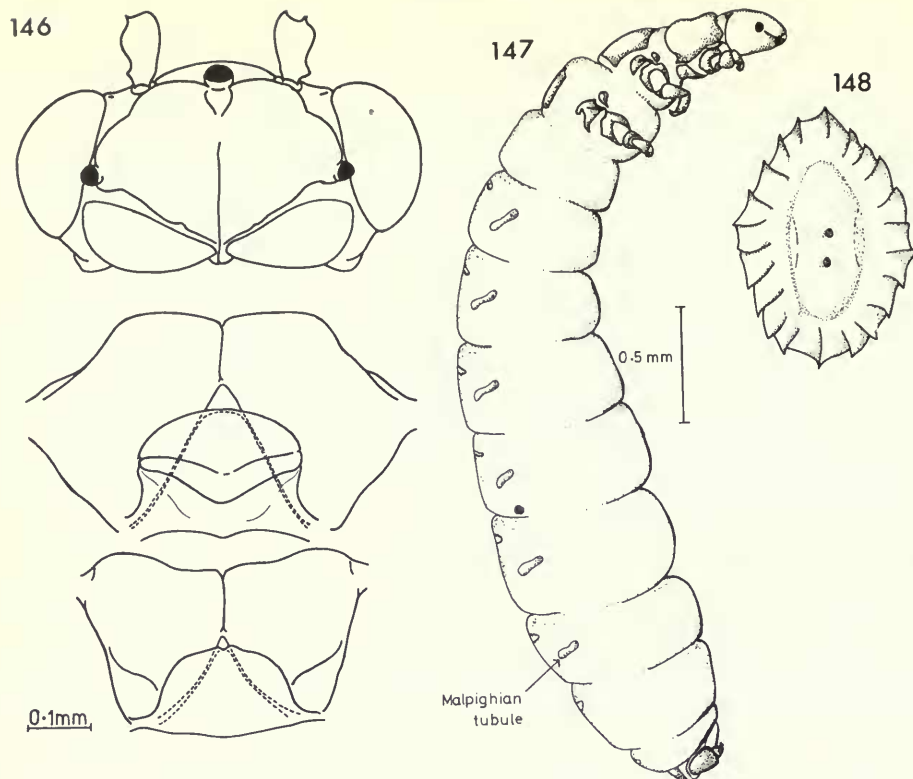
The genus is unique within the Hydroptilidae with respect to the very distinctive male genitalia, the corresponding parts of which, as noted by Sykora, are difficult to homologize with those of any other genus. The following diagnosis is based on Sykora (1967) and examination of Ross's material (the larvae have not previously been described).

DIAGNOSIS. *Adult.* Forewing length 2.5–3.0 mm: head unmodified; tentorium complete; antennae c. 30-segmented: wings elongate, tapering to narrow apex; base of forewing with costal area thickened with a dense fringe of black androconia, oval patch of androconia between Cu_1 and Rs in centre of wing (males): mesoscutellum without transverse suture: spur formula 0.3.4: ♀ genitalia an oviscapt: ♂ genitalia characterized by the inferior appendages ('claspers' (Sykora, 1967)) which are 'bean-shaped' with dorsal and ventral lobes; 'subgenital plate' of Sykora with two long rods; tergite X short, membranous; aedeagus simple, long, rod-like.

Larva (Fig. 147). Head relatively short, wide posteriorly, narrowing anteriorly; 'postmental sclerites' difficult to interpret, but apparently U-shaped: body somewhat compressed dorso-ventrally: thorax widest at segment III; mid- and hind-legs held out more to side than in, for example, *Hydroptila*; legs short, subequal; tibia of each leg with a short apico-ventral process bearing two stout, blunt spines; tarsal claw very small, hook-like; preepisternite free on all segments, epimeron of each apparently fused; single pair of anal sternites present on prothoracic venter only: abdomen not greatly distended, tapering slightly back from metathorax; intersegmental grooves distinct; dorsal 'rings' present on segments II–VIII; in dorsal view the Malpighian tubules can be seen just under the abdominal cuticle, one pair passes along the abdomen laterally and has a distinct loop in each of segments II–VII (possibly having some special osmoregulatory or excretory function ?); tergite IX present; anal prolegs fused to sides of segment X.

Case (Fig. 148). This consists of secretion only and is dorso-ventrally compressed with a central tubular section (in which the larva lives) surrounded by a folded lateral fringe by which the case is probably fixed to the substrate. The central region has two small dorsal holes (possibly to aid water circulation) and the whole case characteristically 'curls up', at least in fluid-preserved specimens.

BIOLOGY. There are no data available on this subject but, from the general appearance of the larva and its case, the genus would seem to be associated with fast-running water habitats (case fixed and flattened).



Figs 146–148 Incertae sedis. 146, *Nothotrichia*, adult head and thorax, dorsal view. 147–148, *Caledonotrichia*; (147) larva, lateral view; (148) case, dorsal view.

DISCUSSION. *Caledonotrichia* is a very distinct hydroptilid genus both with respect to the adult and immature stages, neither of which provide any clues as to the relationships of the group. It would appear to have evolved in complete isolation on the island of New Caledonia to which it is endemic.

Genus *ELECTROTRICHIA* Ulmer

Electrotrichia Ulmer, 1912a : 42. Type-species: *Electrotrichia subtilis* Ulmer, by monotypy.

DISTRIBUTION. Baltic Amber (therefore possibly Eocene, of western Palaearctic origin).

This genus is known from specimens of the type-species in Baltic Amber only; no material was available for examination. From Ulmer's original description (ocelli present; spur formula 0.3.4; forewing length 2.0–2.6 mm; male genitalia figured) it is impossible to place the genus with any certainty within the Hydroptilidae, although the narrow tapering wings and spur formula suggest that it may have affinities with the Hydroptilinae.

Phylogeny of the Hydroptilidae

The family Hydroptilidae may be derived from a primitive glossosomatid-like ancestor early in the evolutionary history of the Trichoptera. Unlike the typical glossosomatids which construct a primitive 'saddle-type' transportable case, the larvae of these early hydroptilid ancestors probably adopted the more advanced type of 'purse-like' case. This basic ancestral stock then appears to have given rise to two distinct lines which have resulted in the present-day subfamilies, the Ptilocolepinae and the Hydroptilinae. The former retained primitive adult features similar to those of the other Rhyacophiloidea, especially the Glossosomatidae, while the latter evolved the more characteristic form associated with present day adult Hydroptilidae.

The larvae of the Ptilocolepinae have retained the basic form of the hypothetical generalized hydroptilid and in addition they exhibit the primitive, cool montane habitat preferences supposedly shown by the early, ancestral Trichoptera. Thus the Ptilocolepinae are now restricted to cool springs in shaded forest regions in the mountainous areas of western Europe and North America. In the Hydroptilinae, on the other hand, the present-day success of the subfamily may be due to the adaptive radiation of the larval stages into a wide variety of freshwater aquatic habitats. These range from springs and seeps to the larger, moderately flowing rivers and streams. Certain groups have become structurally, behaviourally and physiologically adapted for living in conditions requiring specialized modifications. These include the splash zones of waterfalls and rapids, exposed substrates in the more rapid sections of rivers and streams and, at the other extreme, vegetation thickets in slowly moving to almost static, larger bodies of water.

An early member of the ancestral Hydroptilinae stock possibly gave rise to two, or perhaps three, subsidiary evolutionary lines. The first led to the Stactobiini and possibly also the Leuco-trichiini, although it is more likely that the latter arose from a distinct, but closely related, ancestor. The second line eventually radiated into the Ochrotrichiini, Neotrichiini, Hydroptilini and Orthotrichiini which appear to have diverged relatively more recently but which have each undergone such remarkable larval morphological modifications in relation to habitat specialization that the larvae at least are quite distinct. A study of both fundamental adult and larval characters has revealed a number of basic relationships between the four last mentioned tribes which, although not yet fully satisfactorily resolved, are suggestive of the following evolutionary pathways.

The early ancestors of the second (third ?) branch of the Hydroptilinae may have given rise to two distinct and independent Nearctic–Neotropical tribes, the Ochrotrichiini and the Neotrichiini. This may have occurred before the larvae adopted associations with green filamentous algae as is typical of the remaining two tribes, the Hydroptilini and the Orthotrichiini. The latter tribe would appear to be the most advanced tribe since the larvae are highly specialized algal feeders, at least in *Orthotrichia*, and are often capable of tolerating stagnant and polluted conditions.

The relationships of the genera and generic groups within each tribe have been discussed in the relevant sections of the systematic account. The evolutionary steps have been summarized in Chart II.

Genera here transferred from the Hydroptilidae

As a result of a study of all genera previously attributed to the Hydroptilidae the following three small, geographically restricted groups are considered to belong to other Trichopteran families as indicated.

Padunia Martynov, 1910 (= *Uenotrichia* Tsuda, 1942); to GLOSSOSOMATIDAE: PROTOPTILINAE.

Tsukushitrichia Kobayashi, 1964; possibly a synonym of *Kibuneopsychomyia* Tsuda, 1942; to PSYCHOMYIIDAE.

Petrotrichia Ulmer, 1910; possibly related to the primitive, unplaced African genera *Petrothrincus* Barnard and *Hydrosalpinx* Barnard.

Material examined: *Padunia* spp. (loaned from the Lepneva collection, ZI); *Petrotrichia palpalis* Ulmer, paratypes, BMNH; the transfer of *Tsukushitrichia* is based on a study of the original description and figures, material being unavailable for study.

Genus *PADUNIA* Martynov (Glossosomatidae: Protoptilinae)

Padunia Martynov, 1910 : 425. Type-species: *Padunia adelungi* Martynov, by monotypy.

Uenotrichia Tsuda, 1942 : 228. Type-species: *Uenotrichia fasciata* Tsuda, by monotypy. [Synonymized by Fischer, 1971.]

DISTRIBUTION. Asia (central and eastern U.S.S.R.; Korea).

This small Asian genus contains four species described by Martynov from the U.S.S.R. (*adelungi*, *forcipata*, *lepnevae* and *bikinensis*) and one from Korea originally described as *Uenotrichia fasciata* Tsuda. Fischer (1971) synonymized these two genera but wrongly gave preference to *Uenotrichia* since *Padunia* clearly should have date priority.

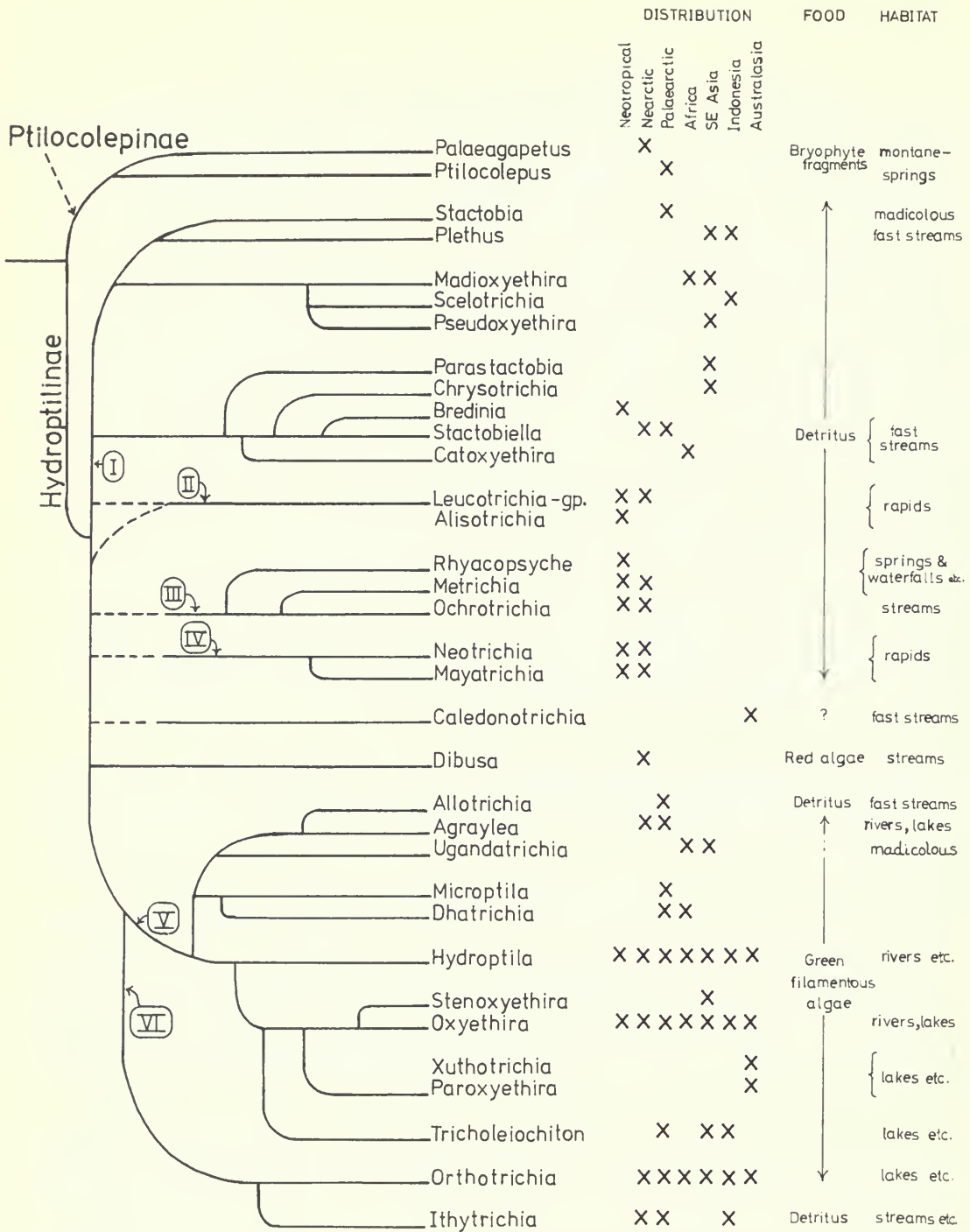


Chart II The phylogeny of the Hydroptilidae: generic relationships (I, Stactobiini; II, Leucotrichiini; III, Ochrotrichiini; IV, Neotrichiini; V, Hydroptilini; VI, Orthotrichiini).

Examination of adult features indicates that *Padunia*, especially with respect to the structure of the thorax, the male genitalia and the shape and venation of the wings, is closely related to *Matrioptila* Ross and *Nepaloptila* Kimmins, primitive members of the Protoptilinae (Glossosomatidae) from the SE. United States and SE. Asia respectively. Figs 149, 150 show the resemblance of the head and thorax of *Padunia* to those of *Nepaloptila*.

In 1954, Mosely transferred *Mortoniella* Ulmer, *Protoptila* Banks, *Mexitrichia* Mosely, *Canoptila* Mosely and *Antoptila* Mosely, which are essentially Neotropical genera, from the Hydroptilidae to the Glossosomatinae, then a subfamily of the Rhyacophilidae. Subsequently, Ross (1956) elevated the group, with the inclusion of *Culoptila* Mosely, to the subfamily Protoptilinae within the Glossosomatidae, at the same time erecting the genus *Matrioptila* for a single primitive species originally described in *Protoptila*.

Representatives of the Protoptilinae occur from southern Canada to central Chile and the subfamily now contains the following additional genera: *Campiophora* Flint, *Cariboptila* Flint, *Mastigoptila* Schmid, *Merionoptila* Schmid and *Tolhuaca* Schmid. The description of *Nepaloptila* Kimmins (1964) from a single Nepalese species furnished the first Palaearctic record of this subfamily and this may now be supported by this discovery of the true identity of *Padunia* Martynov.

Ulmer (*in litt.* to Mosely, *vide* Mosely, 1954) suggested that *Padunia* might also belong with the *Protoptila*-group but, possibly due to not having any material to study, Mosely did not transfer it with the others. He did, however, remark upon its more primitive venation (and its resemblance to *Antoptila*) which is now substantiated if this character is compared with those of *Matrioptila* and *Nepaloptila* which are both considered to be the more primitive members of the Protoptilinae. Ross (1956) considered the subfamily to have originated in the New World due to the occurrence there of *Matrioptila*, but this theory may now need to be modified on account of the discovery of the equally primitive genera *Nepaloptila* and *Padunia* in the Old World. The possibility that *Matrioptila* and *Padunia* were derived from New World ancestors which passed into Asia, however, cannot be ruled out. The immature stages of *Padunia* are unknown.

Genus *TSUKUSHITRICHIA* Kobayashi (Psychomyiidae)

Tsukushitrichia Kobayashi, 1964 : 211. Type-species: *Tsukushitrichia forficula* Kobayashi, by monotypy.

DISTRIBUTION. Japan.

Kobayashi originally described this monotypic genus in the Hydroptilidae but stated that it was unique within the family on account of its atypical spur formula (2.4.3), the structure of the fifth abdominal segment and the wing venation. In addition ocelli are absent, the fifth segment of the maxillary palp is long and flexible and the male genitalia are quite unlike those of any other hydroptilid.

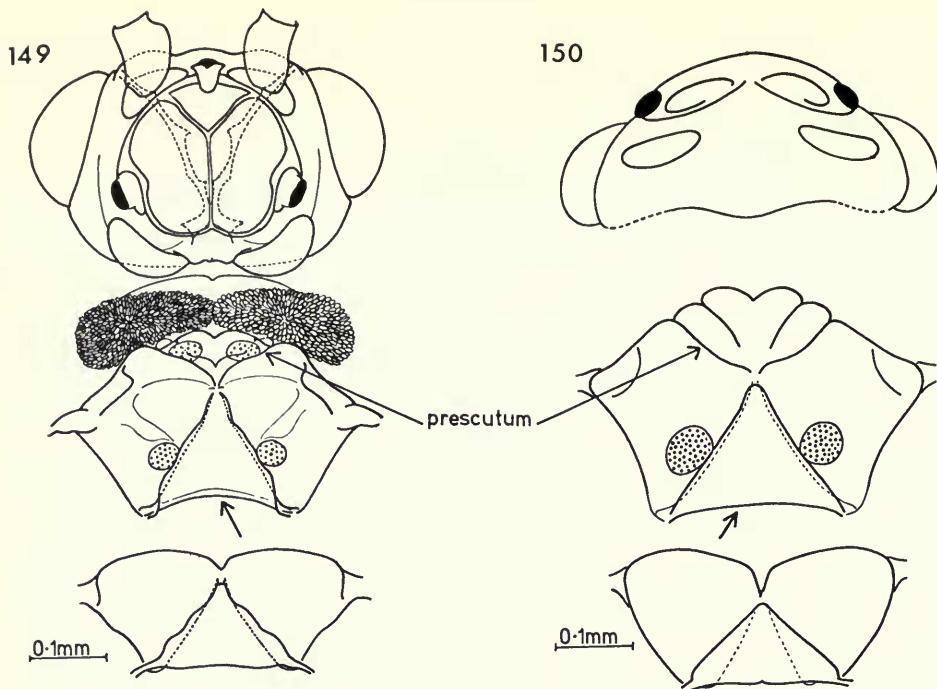
If the spur formula is considered to be derived from the combination 2.4.4, the species keys out in Ross (1944) to the family Psychomyiidae, very close to the genus *Psychomyia* especially with respect to the wing venation and the distinctive elongate fifth segment of the maxillary palp, the latter always being proportionately shorter in the Hydroptilidae. Of the known species of Japanese psychomyiids, *Kibuneopsychomyia kibuneana* Tsuda bears most resemblance to *T. forficula*, both in the venation, which is almost identical, and the general aspect of the male genitalia. It is thus proposed that the genus *Tsukushitrichia* be transferred from the Hydroptilidae to the Psychomyiidae where it may be synonymous with the genus *Kibuneopsychomyia* Tsuda. Examination of material would be necessary to confirm these propositions. Neither the immature stages of *Tsukushitrichia* nor *Kibuneopsychomyia* are known.

Genus *PETROTRICHIA* Ulmer

Petrotrichia Ulmer, 1910 : 43. Type-species: *Petrotrichia palpalis* Ulmer, by monotypy.

DISTRIBUTIONS. Seychelles.

This isolated monotypic genus is known only from the original series of males and females from



Figs 149–150 Glossosomatidae, Protoptilinae, adult head and thorax. 149, *Nepaloptila*; 150, *Padunia*.

the Seychelles, the immature stages being unknown. Examination of paratype material in the BMNH indicates that this genus is definitely not a member of the Hydroptilidae, in which it was originally placed, although difficulty has been encountered in assigning it to its proper family.

The adult features are as follows: head without ocelli or postoccipital warts; basal antennal segment elongate; maxillary palpi (male and female) 5-segmented (cf. Ulmer, 1910); spur formula originally stated to be 0.2.4 but a minute spur has been detected on the fore-tibia, hence 1.2.4; mesothorax elongate (cf. Hydroptilidae), mesoscutellum ovoid, with a short distance between posterior margins of mesoscutellum and notum; metascutellum elongate, subtriangular; wings with rounded apices (slightly tapered); abdominal sternite V without lateral setate processes or sternal ridge; ♂ tenth segment fused, with a pair of parallel, tapering, ventro-lateral processes (= fused inferior appendages), dorsal cerci each with a short median process and longer lateral baso-ventral processes, aedeagus 'fan-like'.

Following Scott's (1967) key to South African caddis-flies, *Petrotrichia* keys out with *Hydrosalpinx* Barnard and *Petrothrincus* Barnard which have been placed in the Beraeidae and Molanidae respectively. The head and thorax of *Petrotrichia* accord well with those of *Molanna flavicornis* as figured by Wiggins (1968 : 11, Fig. 12). Professor H. H. Ross (pers. comm.) is at present studying the relationships of *Hydrosalpinx* and *Petrothrincus* which may prove, at least in the case of the latter, to be primitive relict Trichoptera so far found only in the southern African continent. Ross agrees (pers. comm.) that it is possible that *Petrotrichia* might be a beraeid or a small molannid, especially with respect to the 'weird dorsal processes (cerci)' and the venation. Discovery of the immature stages would greatly aid in establishing the relationships of these genera.

Although such a conclusion is very unsatisfactory, it is proposed that *Petrotrichia* should be removed from the Hydroptilidae, on the basis of the great differences in the structures of the head, antennae, thorax, abdominal segment V and the male genitalia, and that it should be grouped, for the time being, with *Hydrosalpinx* and *Petrothrincus*.

Checklist of species of Hydroptilidae

(* indicates material examined; † indicates fossil species)

Family HYDROPTILIDAE Stephens

Subfamily PTILOCOLEPINAE Martynov

Genus *PTILOCOLEPUS* Kolenati

- **colchicus* Martynov
- **extensus* McLachlan
- **granulatus* (Pictet)
- dilatatus* Martynov
- turbidus* Kolenati
- villosus* Navás

Genus *PALAEAGAPETUS* Ulmer

- **celsus* Ross
- guppyi* Schmid
- nearcticus* Banks
- †*rotundatus* Ulmer

Subfamily HYDROPTILINAE Stephens

Tribe STACTOBIINI Botosaneanu

STACTOBIA-groupGenus *STACTOBIA* McLachlan

- Afrित्रichia* Mosely
- Aratrित्रichia* Mosely
- Lamonganotrichia* Ulmer syn. n.
- furcata*-group
- **algira* Vaillant
- **atra* (Hagen)
- **beatensis* Mosely
- **caspersi* Ulmer
- decostrai* Jacquemart
- **eatoniella* McLachlan
- oredonensis* Mosely
- eretziana* Botosaneanu & Gasith
- freyi* Nybom
- **furcata* Mosely

fuscicornis Schneider sensu
McLachlan, 1884 (partim)

- **fuscicornis* (Schneider)
- obscura* (Kolenati)

jacquemarti Malicky

- **kimminsi* Schmid

- **maculata* Vaillant

- **malacantosa* Schmid

margalitana Botosaneanu

- **mclachlani* Kimmins

botosaneanui Schmid
delamerei Coineau & Jacquemart

fuscicornis Schneider sensu
McLachlan, 1884 (partim)

monnioti Jacquemart

- **moselyi* Kimmins

eatoniella McLachlan sensu
Mosely

fuscicornis Schneider sensu
McLachlan

nybomi Schmid

atra (Hagen) sensu Morton
atra (Hagen) sensu Nybom
atra (Hagen) sensu Schmid

storai Nybom*martynovi*-group

- **dohleri* Schmid
- fischeri* Schmid
- **forsslundi* Schmid
- klapaleki* Schmid
- marlieri* Schmid
- **martynovi* Schmid
- **mayeri* Schmid
- olgae* Martynov
- **quadrispina* Kimmins
- **schmidi* Kimmins
- **tjederi* Schmid
- ulmeriana* Schmid
- urania* Malicky

nielseni-group

- bolzei* Jacquemart
- **crassa* (Ulmer) comb. n.
- **fahjia* (Mosely)
- moretti* Schmid
- **nielseni* Schmid
- radavanovici* Schmid
- risiana* Schmid

vallanti-group

- **aurea* (Mosely)
- **vallanti* Schmid

Incertae sedis

- japonica* Iwata
- mallorcensis* Vaillant (nomen nudum)
- megalatlantica* Vaillant (nomen nudum)

Genus *PLETHUS* Hagen*Plethotrichia* Ulmer syn. n.

- **acutus* Ulmer
- amogawarsa* Schmid
- **baliana* (Ulmer) comb. n.
- **bodikatuwa* Schmid
- cilamegha* Schmid
- cruciatu* Ulmer
- **cursitans* (Hagen)
- kala* Schmid

usawasadenna Schmid
**vajhrobodhi* Schmid
STACTOBIELLA-group
 Genus **STACTOBIELLA** Martynov
Tascobia Ross
biramosa-group
biramosa Martynov
**palmata* (Ross)
ulmeri-group
delira (Ross)
**ulmeri* (Siltala)
risi (Felber)
brustia-group
brustia (Ross)
 Genus **BREDINIA** Flint
dominicensis Flint
 Genus **CHRYSOTRICHIA** Schmid
**aranuwa* Schmid
badhami Schmid
**dotalugola* Schmid
hapitigola Schmid
**hatnagola* Schmid

Genus **PARASTACTOBIA** Schmid
talakalahena Schmid
 Genus **CATOXYETHIRA** Ulmer
Sperotrichia Marlier syn. n.
**fasciata* Ulmer
formosae (Iwata)
**improcera* Statzner
mali (Marlier) comb. n.
**ocellata* Statzner
**pinheyi* Kimmins
veruta Morse
MADIOXYETHIRA-group
 Genus **MADIOXYETHIRA** Schmid
**marshalli* Statzner
**milinda* Schmid
**nepalensis* Kimmins
trifurcata (Jacquemart) comb. n.
 Genus **PSEUDOXETHIRA** Schmid
asgirkanda Schmid
 Genus **SCELOTRICHIA** Ulmer
**saranganica* Ulmer

Tribe LEUCOTRICHINI Flint

LEUCOTRICHIA-group
 Genus **LEUCOTRICHIA** Mosely
melleopicta-group
chiriquiensis Flint
gomezi Flint
**limpia* Ross
**melleopicta* Mosely
tubifex Flint
viridis Flint
pictipes-group
fairchildi Flint
imitator Flint
pictipes (Banks)
sarita Ross
 Genus **ZUMATRICHIA** Mosely
multisetosa-group
multisetosa Flint
galtena-group
antilliensis Flint
attenuata Flint
bifida Flint
chiriquiensis Flint
diamphidia Flint
echinata Flint
**galtena* Mosely
notosa (Ross)
saluda Flint
strobilina Flint
vieja Flint
filosa-group
caudifera Flint
**filosa* Mosely
rhampoides Flint
teapa Flint

palmaria-group
anomalopectera Flint
palmaria Flint
 Genus **PELTOPSYCHE** Müller
maclachlani Müller
**sieboldii* Müller
 Genus **ANCHITRICHIA** Flint
spangleri Flint
 Genus **COSTATRICHIA** Mosely
simplex-group
simplex Flint
spinifera Flint
lodora-group
bipartita Flint
**lodora* Mosely
panamensis Flint
tripartita Flint
 Genus **ACOSTATRICHIA** Mosely
brevipenis Flint
fimbriata Flint
**plaumanni* Mosely
**simulans* Mosely
spinifera Flint
 Genus **BETRICHIA** Mosely
argentinea Flint
bispinosa Flint
occidentalis Flint
surinamensis Flint
**zilbra* Mosely
 Genus **ABTRICHIA** Mosely
**antennata* Mosely
**squamosa* Mosely
 Genus **CELAENOTRICHIA** Mosely
**edwardsi* Mosely

ALISOTRICHIA-groupGenus **ALISOTRICHIA** Flint

argentilinea Flint
blantoni Flint
chorra Flint
dominicensis Flint
hirudopsis Flint

lobata Flint
orophila Flint
quemada Flint
septempunctata Flint
tamaza Flint
trifida Flint
wirthi Flint

Tribe **OCHROTRICHIINI** trib. n.Genus **OCHROTRICHIA** Mosely*Polytrichia* SibleySubgenus **OCHROTRICHIA**

**aldama* (Mosely)
alexanderi Denning & Blickle
alsea Denning & Blickle
**anisca* (Ross)
argentea Flint & Blickle
arizonica Denning & Blickle
**arranca* (Mosely)
**arva* (Ross)
attenuata Flint
brayi Flint
buccata Denning & Blickle
caimita Flint
caligula Flint
capitana Ross
chiapa Denning & Blickle
confusa (Morton)
**contorta* (Ross)
cruces Flint
dactylophora Flint
denningi Blickle & Morse
eliaga (Ross)
escoba Flint
felipe Ross
filiforma Flint
flagellata Flint
gurneyi Flint
hadria Denning & Blickle
ildria Denning & Blickle
**insularis* Mosely
intermedia Flint
lobifera Flint
**logana* (Ross)
**lometa* (Ross)
lucia Denning & Blickle
marica Flint
**mono* (Ross)
moselyi Flint
nacora Denning & Blickle
okanogensis Flint
oregona (Ross)
pacifica Flint
palitla Flint
panamensis Flint
pectinata Flint
pectinifera Flint
phenosa Ross
ponta Flint

potomus Denning
provosti Blickle
quadrispina Denning & Blickle
riesi Ross
rothi Denning & Blickle
shawnee (Ross)
spinosa (Ross)
spinosissima Flint
spinulata Denning & Blickle
**stylata* (Ross)
susanae Flint & Herrmann
tagala Flint
tarsalis (Hagen)
**tenanga* (Mosely)
**trapoiza* Ross
**unio* (Ross)
verda Flint
vertreesi Denning & Blickle
weddleae Ross
wojcickyi Blickle
xena (Ross)
zioni Denning & Blickle

Subgenus **METRICHIA** Ross

Argentitrichia Jacquemart syn. n.
aberrans Flint
argentinica Schmid
arizonensis Flint
biungulata Flint
bulbosa (Jacquemart) comb. n.
campana Flint
continentalis Flint
dietzi Flint
exclamationis Flint
juana Flint
lemniscata Flint
neotropicalis Schmid
nigritta Banks
penicillata Flint
quadrata Flint
similis Flint
trigonella Flint
warema Flint
yalla Flint

Genus **RHYACOPSYCHE** Müller

hagenii Müller
mexicana (Flint)
obliqua Flint
torulosa Flint
turrialbe Flint

Tribe NEOTRICHINI Ross

Genus *NEOTRICHIA* Morton

Cyllene Chambers
Exitrichia Mosely
Dolotrichia Mosely
Guerotrichia Mosely
Lorotrichia Mosely
collata-group
alata Flint
**anahua* (Mosely)
collata Morton
**digitata* (Mosely)
elerobi Bickel
**eroga* (Mosely)
ersitis Denning
**esmalda* (Mosely)
**exicoma* (Mosely)
falca Ross
heleios Flint
interrupta Flint
iridescens Flint
minutisimella (Chambers)
**notuena* (Mosely)
**novara* (Mosely)
numii Ross
okopa Ross
**olorina* (Mosely)
osmena Ross
**ovona* (Mosely)
**oxima* (Mosely)
panneus Denning
riegeli Ross
sonora Ross

**tertia* (Mosely)
vibrans Ross
ranea Denning
canixa-group
**canixa* (Mosely)
corniculans Flint
**dubitans* (Mosely)
**xicana* (Mosely)
caxima-group
**cameria* (Mosely)
**caxima* (Mosely)
costaricensis Flint
edalis Ross
rotundata Flint
hiaspa-group
halia Denning
**hiaspa* (Mosely)
kitae Ross
biuncifera-group
biuncifera Flint
bullata Flint
falcifera Flint
proboscidea Flint
unispina Flint
bifida-group
bifida Flint
lobata Flint

Genus *MAYATRICHIA* Mosely

acuna Ross
**ayama* Mosely
ponta Ross
**rualda* Mosely

Tribe HYDROPTILINI Stephens

AGRAYLEA-groupGenus *AGRAYLEA* Curtis

argyricola Kolenati
**cognatella* McLachlan
costello Ross
drosima Navás
insularis (Hagen)
**multipunctata* Curtis
multiguttata Uljanin
signata Banks
flavida (Banks)
fraterna Banks
saltesea Ross
**sexmaculata* Curtis
pallidula McLachlan
flabellifera (Bremer) (partim)

†*spathifera* Ulmer

Genus *ALLOTRICHIA* McLachlan

†*ampullata* Ulmer
heterocera Navás
laerma Malicky

marinkoviciae Malicky
**pallicornis* (Eaton)
succinica Hagen
tauri Jacquemart
teldanica Botosaneanu
vilnensis Raciecka

Genus *MICROPTILA* Ris

apsara Schmid
**bejela* Mosely
**indra* Schmid
**minutissima* Ris

Genus *UGANDATRICHIA* Mosely gen. rev.

Moselyella Kimmins
nigra-group
**acuta* Mosely
africana (Marlier & Vaillant) comb. n.
**minor* Mosely
**nigra* Mosely
rhodesiensis Scott
violacea-group
**cyanotrichia* (Kimmins)

- **nikataruwa* (Schmid)
- roudra* (Schmid) **comb. n.**
- **sourya* (Schmid) **comb. n.**
- **violacea* (Morton)

Genus **DHATRICHIA** Mosely

- **bipunctata* Statzner
- **inasa* Mosely

HYDROPTILA-group

Genus **HYDROPTILA** Dalman

- Phrixocoma* Eaton
- Hydropneuma* Enderlein
- Hydroptilina* Martynov
- Oxydroptila* Martynov **syn. n.**
- Oeceotrichia* Ulmer **syn. n.**
- Pasirotrichia* Ulmer **syn. n.**
- Sumatranotrichia* Ulmer **syn. n.**

sparsa-group

- **acuta* Mosely
- **africana* Kimmins
- **angulata* Mosely
- **campanulata* Morton
- cintrana* Morton
- **cornuta* Mosely
- emarginata* Martynov
- friedeli* Malicky
- **fuentaldeala* Schmid
- **hochyangha* Schmid
- **lotensis* Mosely
- **simulans* Mosely
- **sparsa* Curtis

uncinata-group

- angulifera* Kumanski
- **fortunata* Morton
- juba* (Enderlein)
- insubrica* Ris
- kalonichtis* Malicky
- buresschi* Kumanski
- **stellifera* Morton
- **sylvestris* Morton
- **uncinata* Morton
- vichtaspa* Schmid

capensis-group

- calundoensis* Marlier
- **capensis* Barnard

consimilis-group

- **ajax* Ross
- albicornis* Hagen
- maculata* (Banks)
- transversa* Banks

ancistrion Flint

- **angusta* Ross
- antillarum* Flint
- arctia* Ross
- berneri* Ross
- broweri* Blickle
- **consimilis* Morton
- denza* Ross
- ditalea* Flint
- grenadensis* Flint

- **icona* Mosely
- latosa* Ross
- lloganae* Blickle
- martorelli* Flint
- medinai* Flint
- **melia* Ross
- **meralda* Mosely
- **mexicana* Mosely
- novicola* Blickle & Morse
- **paschia* Mosely
- **pecos* Ross
- **perdita* Morton
- **producta* Mosely
- pullatus* Denning
- quinola* Ross
- scolops* Ross
- strepha* Ross
- surinamensis* Flint
- tusculum* Ross
- valhalla* Denning
- veracruzensis* Flint

occulta-group

- **adana* Mosely
- **armata* Ross
- **cognata* Mosely
- **cruciata* Ulmer
- **gandhara* Schmid
- **hirra* Mosely
- **martini* Marshall
- occulta* (Eaton) **sensu auctt.**
- **occulta* (Eaton)
- insignis* Martynov
- **kimminsi* Mosely
- **parthava* Schmid

palestiniae Botosaneanu & Gasith

- panchaoi* Schmid
- phaon* Malicky
- rhodica* Jacquemart
- kumanskii* Malicky

- **sanghala* Schmid
- **spatulata* Morton
- taurica* Martynov
- **vala* Ross
- **valesiaca* Schmid
- waskesia* Ross

tineoides-group

- amoena* Ross
- **ampoda* Ross
- callia* Denning
- fiskei* Blickle
- **hamata* Morton
- perplexa* Mosely
- lennoxii* Blickle
- metoeca* Blickle & Morse
- **modica* Mosely
- moselyi* Ulmer
- remita* Blickle & Morse
- **rono* Ross
- spinata* Blickle & Morse

**tineoides* Dalman
femoralis (Eaton)
longispina McLachlan
tortosa Ross
wyomyia Denning
dikirilagoda-group
dikirilagoda Schmid
**kurukepitiya* Schmid
mitirigalla Schmid
losida-group
**bispina* Kimmins
**incertula* Mosely
**losida* Mosely
**tasmanica* Mosely
**triloba* Kimmins
pulchricornis-group
aegyptia Ulmer
**dampf* Ulmer
kurnas Malicky
phenianica Botosaneanu
**pulchricornis* Pictet
forcipata-group
**bifurcata* Mosely
**forcipata* (Eaton)
ivisa Malicky
vectis-group
**vectis* Curtis
corsicanus Mosely
maclachlani Klapálek
viganoi Botosaneanu
tigurina-group
**cortensis* Mosely
tigurina Ris sensu Mosely
rheni Ris
**tigurina* Ris
waubesiana-group
**acadia* Ross
**delineata* Morton
nicoli Ross
salmo Ross
wakulla Denning
**waubesiana* Betten
xoncla Ross

Incertae sedis

acoma Denning
angustipennis (Martynov)
annulicornis Matsumura
**argosa* Ross
**armathai* Schmid
brincki Jacquemart
crenata (Ulmer) **comb. n.**
decia Etnier & Way
dentata Ross
dodgei Denning
elongata (Ulmer) **comb. n.**
eramosa Harper
fuentelarbola Schmid
furcata (Martynov) **comb. n.**
grandiosa Ross

gunda Milne
jackmanni Bickler
kirilawela* (Schmid) **comb. n.
lonchera Bickler & Morse
molsonae Bickler
pectinifera Schmid
†phileos Cockerell
**protera* Ross
sengavi Schmid
**serrata* Morton
simplex Nielsen (doubtful sp. acc.
 Nielsen, *in litt.*)
**touroumaya* Schmid
trilobata Jacquemart
trullata (Ulmer) **comb. n.**
usurigonis Matsumura
**virgata* Ross
xella Ross
xera Ross

OXYETHIRA-group

Genus *OXYETHIRA* Eaton

Lagenopsyche Müller
Argyrobothrus Barnard
Loxotrichia Mosely
Dampftrichia Mosely
Oxytrichia Mosely
falcata-group
boreella Svensson & Tjeder
delcourti Jacquemart
dentata Nybom
bidentata Nybom
**falcata* Morton
rhodani Schmid
fischeri Higler
**frici* Klapálek
**spinosella* McLachlan
flavicornis-group
**bogambara* Schmid
campanula Botosaneanu
ecornuta Morton
**flavicornis* (Pictet)
costalis (Curtis) sensu Eaton
sida Bickler & Morse
**tenuella* Martynov
**unidentata* McLachlan
fuentelarbola Schmid
meridionalis Jacquemart & Coineau

rivicola-group

allagashensis Bickler
dualis Morton
**forcipata* Mosely
grisea Betten
lumosa Ross
**michiganensis* Mosely
novasota Ross
obscura Flint
obtatus Denning
rivicola Bickler & Morse
rossi Bickler & Morse

setosa Denning
sodalis Ross & Spencer
unispina Flint
simplex-group
galekoluma Schmid
**harpagella* Kimmins
paramartha Schmid
ramosa Martynov
angustella Martynov
**simplex* Ris
**tristella* Klapálek
distinctella-group
araya Ross
**distinctella* McLachlan
**sagittifera* Ris
**serrata* Ross
azteca-group
archaica Malicky
**azteca* (Mosely)
**dalmeria* (Mosely)
glasa (Ross)
janella Denning
neglecta Flint
puertoricensis Flint
**zilaba* (Mosely)
ulmeri-group
aculea Ross
arizona Ross
cirrifera Flint
tega Flint
**ulmeri* (Mosely)
zeronia-group
jamaicensis Flint
longissima Flint
macrosterna Flint
simulatrix Flint
verna Ross
walteri Denning
zeronia Ross
pallida-group
florida Denning
**maya* Denning
pallida (Banks)
cibola Denning

viminalis Morton
bidentata-group
abacatia Denning
aeola Ross
**bidentata* Mosely
mirabilis-group
flagellata Jacquemart
**mirabilis* Morton
Incertae sedis
**albiceps* McLachlan
anabola Blickle
angustella Martynov
berneri Etnier & Way
coercens Morton
hyalina (Müller)
incana Ulmer
spirogyrae (Müller)
**velocipes* (Barnard)
Genus *STENOXYETHIRA* Kimmins
Gnathotrichia Ulmer syn. n.
**excisa* Kimmins
**isabellina* (Ulmer) syn. n.
**minima* Kimmins
Genus *PAROXYETHIRA* Mosely
**eatoni* Mosely
**hendersoni* Mosely
hintoni Leader
kimminsi Leader
**tillyardi* Mosely
Genus *XUTHOTRICHIA* Mosely
**eskensis* Mosely
**fimbriata* Mosely
**ochracea* Mosely
**simplex* Mosely
Genus *TRICHOLEIOCHITON* Kloet & Hincks
Leiochiton Guinard
Synagotrichia Ulmer syn. n.
**fagesii* (Guinard)
felina (Ris)
flabellifera (Bremi) partim.
**fortensis* (Ulmer) comb. n.
**lacustris* Kimmins

Tribe ORTHOTRICHINI Nielsen

Genus *ORTHOTRICHIA* Eaton
Clymene Chambers
Javanotrichia Ulmer syn. n.
Orthotrichiella Ulmer syn. n.
Baliotrichia Ulmer syn. n.
angustella-group
**angustella* (McLachlan)
brunneicollis (Pictet) (partim)
**avicularis* Kimmins
barnardi Scott
benguelensis Marlier

damasi Marlier
dampfi (Ulmer) comb. n.
flagellum Marlier
indica Martynov
kivuensis Jacquemart
melitta Malicky
**moselyi* Tjeder
**sanya* Mosely
**spinicauda* Kimmins
straeßini Jacquemart
verbeki Jacquemart

litoralis-group
**curvata* (Ulmer) comb. n.
guruluhela (Schmid) comb. n.
hinipitigola (Schmid) comb. n.
**litoralis* (Ulmer) comb. n.
**maeandrica* (Ulmer) comb. n.
medipitigola (Schmid) comb. n.
**ranauana* (Ulmer) comb. n.
udawarama (Schmid) comb. n.
costalis-group
**aequatoriana* Kimmins
alboguttata Jacquemart
**costalis* (Curtis)
tetensii Kolbe
extensa Martynov
aegerfasciella-group
**aegerfasciella* (Chambers)
**americana* Banks
dorsalis Banks
brachiata Morton

baldufi Kingsolver & Ross
**cristata* Morton
americana Betten
curta Kingsolver & Ross
instabilis Denning
**tragetti* Mosely
kokodana-group
**kokodana* Kimmins
**obscura* Kimmins
Incertae sedis
dentata Kingsolver & Ross
petiti Jacquemart
trilineata Jacquemart
Genus *ITHYTRICHIA* Eaton
Saranganotrichia Ulmer syn. n.
bosniaca Botosaneanu
**clavata* Morton
**decussata* (Ulmer) comb. n.
**lamellaris* Eaton
brunneicornis (Pictet) (partim)

INCERTAE SEDIS

Genus *MACROSTACTOBIA* Schmid
**elawalikanda* Schmid
Genus *DIBUSA* Ross
angata Ross
Genus *NOTHOTRICHIA* Flint
illiesi Flint
Genus *DICAMINUS* Müller
Diaulus Müller
ladislavii (Müller)

Genus *ORPHNINOTRICHIA* Mosely
**maculata* Mosely
Genus *CALEDONOTRICHIA* Sykora
**illiesi* Sykora
minor Sykora
Genus *ELECTROTRICHIA* Ulmer
†*subtilis* Ulmer

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